Revision of the Supraspecific Classification of Marginelliform Gastropods

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ABSTRACT

The supraspecific classification of marginelliform gastropods, formerly treated as the single family Marginellidae, is revised. This revision is based on all available information for all Recent species plus a representative sampling of the fossil fauna, and includes all Recent and fossil genus-group names. All published information is summarized, and additional dissections, concentrating on the foregut and radular morphology, are reported, nearly doubling the number of species known anatomically. Fundamental differences between two groups of marginelliform gastropods are discussed. Cystiseids have internal shell whorls partially resorbed and columellar plications reduced internally. Their radular morphology differs fundamentally in having narrower, more numerous rachidian plates, a different subradular membrane structure, separate odontophoral cartilages, and in the plate development on the posterior end. They differ anatomically in the possession of a typical neogastropod radular sac. True marginellids have unmodified internal whorls and columellar plications continuous internally. Their radulae are shorter and broader, odontophoral cartilages are fused anteriorly, and a marginellid buccal pouch is present. The Olividae have the same specializations as the cystiseids and these two groups are considered to have a common ancestry. On this basis, the Cystiseidae is recognized as a valid family and not considered to be closely related to the Marginellidae. The ancestry of the Marginellidae is discussed and the family is considered to be related to the Volutidae. The Cystiseidae is divided into four subfamilies, three of which are described as new. Nine Recent genera, plus one fossil genus, are recognized. *Plesiocystiscus*, new genus, is described on the basis of a triserial radula and other primitive characters. The Marginellidae is divided into two subfamilies and three tribes, two of which are new. A total of 22 Recent genera are recognized in this family, plus nine fossil genera. *Serrataginella*, new genus, is described on the basis of its unique radular and shell morphology. A systematic section lists synonyms and type species of each genus, along with a diagnosis, description, and summaries of the distribution and fossil record. The phylogeny of both families is discussed, and keys to Recent genera in both groups are presented.

Key words: Cystiseidae, Marginellidae, marginelliform gastropods, systematics, supraspecific classification, new genera, new subfamilies, anatomy.

INTRODUCTION

> The best classifications are thus based on the widest possible variety of comparative data.
> Richard E. Blackwelder (1964:25)

The higher classification of the family Marginellidae has long been in a state of confusion. Especially useful for an overview of the taxonomic history are the papers of Coan (1965) and Coomans (1976). The early monographs of G. B. Sowerby II (1846), Reeve (1864–1865), Weinkauff (1878–1879), and Tryon (1882–1883), as well as Tomlin's (1917) catalog, treated all members of this family under the single genus *Marginella*. Many popular works still treat all of them under this single genus, while others use generic names inconsistently or erroneously, basing them primarily on superficial similarities of the shell. Coan's (1965) important reclassification was a major improvement, but is now outdated by new information. The confusion over the classification stems from the fact that shell characters alone were used in the early classifications, or were largely used in later classifications. Although many good conchological characters exist, they have generally been misinterpreted, or, in some cases, unrecognized. Information on radulae and external anatomy was widely scattered in the literature, and internal anatomical data, only recently available, is represented by a very small sample.

The senior author has spent the last 13 years working toward a revision of the supraspecific classification of the family Marginellidae on a world-wide basis, studying all aspects of these animals, including shell characters, external anatomy, radulae, internal anatomy, and observations of live animals, including egg capsules. During this process, many new characters were discovered. We feel enough information has finally been gathered that a stable supraspecific classification can be presented, summarizing this research and presenting a complete classification, including complete synonymies of all Recent and fossil genus-group names, along with an interpretation of the phylogeny of this group.

MATERIALS AND METHODS

Since most species were originally described on the basis of the shell, this character complex is of primary importance. Because the eventual aim is to completely monograph this group at the species level, initial work involved acquiring every original description for each Recent species named, as well as all significant subsequent descriptions. A comprehensive species list was compiled from the main catalogs of the family (i.e. Redfield, 1870; Tomlin, 1917; Wagner & Abbott, 1978) and all issues of The Zoological Record and other standard nomenclators were consulted, resulting in the publication of a comprehensive bibliography (Coovert, 1988e). This body of information primarily dealt with the shell, and much effort was expended on studying and analyzing the conchological characters of all Recent species (Coovert, 1988d). The type species of all genus-group taxa were closely scrutinized (Coovert, 1986a, 1986b, 1986d, 1986e, 1987a, 1987c, 1987d, 1987f, 1987h, and 1988b). A vast amount of information was accumulated, including the original descriptions of every nominate species, most subsequent descriptions, a large number of photographs of type specimens and other material, drawings, tabular sheets recording locality data and shell measurements for thousands of specimens, keys to species groups, graphs of morphometric shell data, comparative charts, and personal observations and notes. All taxa were provisionally determined to be valid, synonymous, or undescribed, and subsequently assigned to a genus. Further research refined these synonymies and generic allocations. From this large database, a comprehensive species catalog of every valid Recent species was compiled, basing all generic allocations and synonymies on the work outlined herein, not on previous assignments. The generic descriptions, diagnoses, and species counts contained in the systematic section of this paper are summarized from this database. A total of 766 valid Recent species, including 77 undescribed species, is currently recognized for this entire group.

Literature on fossil species was not as comprehensively studied as that on the Recent fauna, but the original descriptions of all genus-group names were studied and a clear determination of each type species was made. A large sampling of additional literature on fossil species was obtained and studied, representing all regions worldwide. Specimens and descriptions of fossil species from the western Atlantic were particulary well represented. Generic allocations of fossil species are based on our own work, and do not necessarily agree with previous assignments. Our approach to the fossil fauna is conservative. Only specimens or literature personally examined were included in our database. A good representation of the fossil fauna has been obtained, and is presumed complete as far as genus-group names are concerned.

During this 13-year period, shell specimens from a wide variety of sources, including a large number of museums and individuals (see acknowledgements), were studied, largely concentrating on the Recent fauna.

Shell measurements, including maximum length parallel to the axis and maximum width perpendicular to the axis, were made with a Spencer AO binocular dissecting microscope using a calibrated optical reticle for minute to small shells under 5 mm. For larger shells, an electronic digital Max-Cal caliper was used with a resolution to 0.01 mm. Internal plications were initially studied by noting internal features on shells with gastropod drill holes or breakage. More detailed studies were conducted by grinding a hole on the ventral surface of the shell with a fine metal file. Some shells were transversely sectioned with a fine jeweler's saw, ground to a smooth surface on a fine-grit whetstone, then polished on a glass plate with toothpaste as a fine abrasive.

Methods used for the extraction, illustration, and analysis of radulae are given in complete detail in Coovert and Coovert (1987) and only summarized here. Most radulae were extracted without damaging the shell by soaking and flushing the shell with a solution of 10% potassium hydroxide (KOH) using a micropipette. After rinsing with acidic water, radulae were transferred to a microscope slide and mounted in glycerin jelly. Drawings were made using an optical reticle grid in a standard light microscope. Radular data, reported for each genus in the systematic section, includes a shell length to radular width ratio plus the Radular Index. The Radular Index is derived by dividing the number of rachidian plates by the number of cusps per plate, and requires a complete radular ribbon, which was not always available. Routine extraction using KOH destroys many details of the delicate subradular membrane, especially in true marginellids. For a detailed study of these features, radulae were removed during dissection without the use of KOH and studied in glycerin before mounting (see below). Study of the developing posterior end of the radula was made from previously mounted material. All personally prepared material, totalling 224 specimens of 97 species, was mounted using glycerin jelly and studied with a standard microscope. Through the courtesy of Dean Hewish, SEMs of radulae from 99 specimens of 67 mostly Australian species, with complete locality, shell, and morphometric data, were made available. A review and summary of published information is given in Coovert (1989b), with additional radular data presented in Coovert and Coovert (1990). A combined total of 190 radulate species, plus an additional 30 species known to lack a radula, have been studied in detail.

The external anatomy from published sources was summarized in Coovert (1987g). Many photographs and drawings, provided by colleagues, were also studied. Live material was examined using a Spencer AO binocular dissecting microscope, then carefully drawn in color. In more remote localities, a Rupen wide-field 16 X hand lens was used. Photographs were taken when possible. Data on the external anatomy of 183 species is summarized in this paper.

All published data on the internal anatomy was studied in great detail. Charts of potentially useful taxonomic characters of all 13 anatomically known species were

constructed, patterned after those in Harasewych and Kantor (1991). Using this information as a guide, and carefully choosing taxa to augment this published data, dissections were completed on 11 additional species, plus one previously reported species that lacked sufficient data. We concentrated on features of the foregut, as these were determined to be of most value taxonomically. Specimens were dissected using a Spencer AO binocular dissecting microscope. Gross dissections were completed on multiple specimens of a species when available, with a total of 26 specimens being dissected (Table 1). Detailed, annotated drawings were made during all stages of dissection. Preservation varied among material due to a wide range of sources and preservatives. Larger animals were extracted from shells with a fine jet of water after briefly soaking them in liquid dish soap. Smaller shells were first measured, then cracked using a small hand vice. Odontophoral cartilages were carefully extracted from the buccal mass of radulate species, manually cleaned of adherent tissue, and mounted on microscope slides using glycerin jelly as a mounting medium. The subradular membranes of these radulae were cleaned of extraneous tissue after extraction and studied in glycerin prior to permanent mounting in glycerin jelly. Potassium hydroxide was not used in the preparation of these cartilages or radulae at any stage. A list of the dissected material, with locality data, shell measurements, and other details, is presented in Table 1.

The following revision is based on all available information of every Recent species plus a representative survey of the fossil fauna. Most importantly, the type species of all marginelliform genus-group names, both Recent and fossil, were studied and fully clarified. Genera are based on groups of related species, not just their type species. A very conservative attitude was taken towards recognition of higher taxa. Shared, derived characters were searched for to unite groups rather than using minor differences to split groups. The rank of subgenus is not utilized in the classification presented as this would require additional research and necessitate formal recognition of additional taxa. We prefer the useage of informal "species groups." The proposal of new taxa has been avoided unless strongly supported.

ABBREVIATIONS AND CONVENTIONS

The following abbreviations and conventions are used in the systematic section and text:

=?	synonymy questioned (species)
?	synonymy questioned (genus)
†	(preceding genus), denotes extinct genus
†	(following species), denotes fossil species
aff.	*affinis*, having affinity with but not identical with
AMNH	American Museum of Natural History
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BM(NH)	British Museum of Natural History
DMNH	Delaware Museum of Natural History
GAC	collection of Gary A. Coovert
ICZN	International Code of Zoological Nomenclature
M	original designation by monotypy
MHNG	Muséum d'Histoire Naturelle, Genève
MNHP	Muséum national d'Histoire naturelle, Paris
NMV	National Museum of Victoria
OD	original designation
OD (M)	original designation as type species, but also monotypic
OD (T)	original designation as type species, but also tautonomous
SD	subsequent designation as type
SD (M)	subsequent designation as type species, but also monotypic
sic	to signify exact transcription
T	original designation by tautonomy
TS	type species
USNM	National Museum of Natural History, Smithsonian Institution

In the systematic section, the following sequence is used for each generic synonym:

Genus in original combination, followed by author, year, page number(s)
TS as cited by original author of genus (or if not originally cited, as cited by author of SD)
TS in original combination of author of species, if different from above
Senior synonym if applicable
Designation of type species (i.e. M, OD, OD (M), OD (T), SD, SD (M), T); SD followed by author, year, page number(s)

In the systematic section, *nomina nulla* (misspellings) are not included. Most *nomina nuda*, unless they have a direct bearing, are also not included. Citing these is undesirable because it imparts a false sense of validity. The comments in Tomlin (1917:242) are applicable.

Throughout the remainder of this paper, the term marginellid will be used in the strict sense for the family Marginellidae as defined and restricted in the systematic section herein. The term cystiscid will be used for the family Cystiscidae as defined in the systematic section herein. The term marginelliform will be used in the broad sense of marginellid, equivalent to the traditional concept of the family Marginellidae as conceived by previous authors, and including both marginellids in the strict sense and cystiscids.

Terminology pertaining to shell morphology, radular morphology, and anatomy has been used differently and without standardization by previous authors. Consistency and uniformity are important enough to warrant careful selection and concise definition of terms. In addition, several new terms are introduced and defined.

Table 1. Sex, voucher number, locality data, comments, and shell measurements of dissected material. All dissected specimens, including shells and slide preparations, have been retained in the collection of Gary A. Coovert.

Species	Sex	Vouchers	Locality/Comments	Shell Length (mm)	Shell Width (mm)
Bullata bullata (Born, 1778)	male	GAC Acc. #16-90	Bahia de Todos Santos, Bahia State, Brazil, 5 meters depth, ex. E. C. Rios; ex isopropyl alcohol, Note 1	52.1	27.8
Dentimargo eburneola (Conrad, 1834)	female	GAC 1177A	Stock Island, on N. side of U.S. Rt. 1, E. end of island, Monroe Co., Florida, under algae covered rocks in 0.3 m, Sept. 7, 1984, collectors G. A. & H. K. Coovert; ex isopropyl alcohol	6.9	3.1
Dentimargo eburneola (Conrad, 1834)	male	GAC 1448	Stock Island, on N. side of U.S. Rt. 1, E. end of island, Monroe Co., Florida, hand-dredged in sea grass beds in 0.3 m, Nov 30, 1988, collectors G. A. & H. K. Coovert; ex. isopropyl alcohol	—	—
Hyalina pallida (Linné, 1758)	male	GAC Acc. #4-94 C	(no data); ex. Robert Lipe; ex. ethyl alcohol, animal only	—	—
Marginella glabella (Linné, 1758)	female	GAC M2548	"Banco Canario-Saharia," (apparently a fishing bank between Spanish Sahara and the Canary Islands), March 20, 1991; ex. José Aguiar Morales; ex. methyl alcohol, subsequently softened with trisodium phosphate	41.8	23.8
Marginella sebastiani Marche-Marchad & Rosso, 1979	male	GAC M2549A	(same data as above)	38.8	21.4
Marginella sebastiani	female	GAC M2549C	(same data as above)	39.8	23.4
Persicula interruptolineata (Megerle von Mühlfeld, 1816)	male	GAC 1581A	N. end of Playa La Galera, Isla de Margarita, Venezuela, NE side of bay, hand-dredged on sandy mud with small patches of Turtle Grass, Oct. 22, 1992, collectors G. A. & H. K. Coovert; ex isopropyl alcohol	14.7	9.6
Persicula interruptolineata	female	GAC 1581B	(same data as above)	12.5	8.4
Persicula interruptolineata	female	GAC 1581C	(same data as above)	12.2	7.9
Persicula interruptolineata	female	GAC 1581D	(same data as above)	11.6	7.5
Persicula interruptolineata	female	GAC 1581E	(same data as above)	13.5	8.4
Persicula masirana Roth & Petit, 1972	2 males	GAC Acc. #4-94 A, B	Masirah Island, Oman, shallow water, low tide, collector Donald T. Bosch, ex. Robert Lipe; ex. ethyl alcohol; animals only	—	—
Prunum aff. *aletes* Roth, 1978 Note 2	male	GAC 1518A	small island just off Tamarindo Beach, S. of Tamarindo Diria Hotel, Guanacaste Province, Costa Rica, under rocks, low tide, Oct. 18, 1989, collector Peter Bright; ex. isopropyl alcohol	18.8	12.1
Prunum aff. *aletes*	female	GAC 1518B	(same data as above)	19.4	12.2
Prunum aff. *aletes*	male	GAC 1518C	(same data as above)	20.4	13.4
Prunum guttatum (Dillwyn, 1817)	male	GAC Acc. #2-89	Airport Reef, Utila Island, Bay Islands, Honduras, shallow water under rocks; ex. Robert Lipe, ex isopropyl alcohol; animal only	—	—
Prunum guttatum	male	GAC 1172A	channel behind Lagoon Motel, Marathon, Key Vaca, Monroe Co., Florida, under rocks, snorkeling in 0–1 m, Sept. 5, 1984, collectors G. A. & H. K. Coovert, ex isopropyl alcohol	16.5	9.7
Prunum guttatum	male	GAC 1170B	(same data as above); Sept. 4, 1984, late juvenile	14.8	8.0
Prunum prunum (Gmelin, 1791)	female	GAC 1582	Mata Redonda, Isla de Margarita, Venezuela, shallow sand and mud flats with scattered Turtle Grass, low tide, Oct. 24, 1992; ex John Wolfe; ex isopropyl alcohol	30.7	15.8

Table 1. Continued

Species	Sex	Vouchers	Locality / Comments	Shell Length (mm)	Shell Width (mm)
Prunum roosevelti (Bartsch & Rehder, 1939) Note 3	male	GAC Acc. #26-88A	Walkers Cay, Bahamas, snorkeling at 1 m, grass and algae, night, June 17, 1988, collector Robert Lipe; ex. isopropyl alcohol; animal only	—	—
Prunum roosevelti	male	GAC Acc. #26-88B	(same data as above)	16.9	11.0
Volvarina aff. *avena* (Kiener, 1834) Note 4	male	GAC 1172B	channel behind Lagoon Motel, Marathon, Key Vaca, Monroe Co., Florida, under rocks, snorkeling in 0–1 m, Sept. 5, 1984, collectors G. A. & H. K. Coovert; ex. isopropyl alcohol	11.3	5.0
Volvarina aff. *avena*	female	GAC 1170C	(same data as above); Sept. 4, 1984	11.3	5.0
Volvarina aff. *avena*	female	GAC 1170E	(same data as above); Sept. 4, 1984	10.1	4.5

Note 1: Radula figured in Coovert and Coovert (1990:2, fig. 1).

Note 2: Shells were significantly larger and much more brilliantly and differently colored than the nominate deep-water form (from 3 to 82 m). More research is necessary to establish the status of this taxon.

Note 3: The radula of this species is closest to *P. carneum* (Storer, 1837), the animals greatly differing in the external coloration. The radulae are very distinct from the conchologically very similar *Prunum amabile* (Redfield, 1852), also from the Bahamas, whose radula was described in Coovert and Coovert (1990:5–6).

Note 4: See comments in Coovert and Coovert (1990:35) regarding the status of the Florida form of this species.

COMPARATIVE ANALYSIS OF SHELL MORPHOLOGY

Contrary to the opinion of many previous authors, there are many conchological characters that are very useful in the classification of marginelliform gastropods. Those most useful for higher categories are emphasized.

External varix: The external varix or "margin," for which these shells are named, is one of the more important shell characters. Other authors have used the terms "margin," "marginal varix," "varix," "labial varix," "outer varix," or "varical callus," not clearly differentiating between a true external varix and a merely internally thickened lip. The term external varix is herein used in preference over the above terms as it more clearly makes this differentiation. A shell with an external varix has a weakly to distinctly raised margin of callus deposited externally along the labial edge, easily seen by close dorsal examination of the shell.

In all marginelliforms, the outer lip is at least somewhat strengthened or thickened internally in the adult, but many genera completely lack an external varix. This fact has received very little attention in the literature and most original descriptions fail to mention the presence or absence of this important character. Shells lacking a varix are even and smooth along the external labial edge, without a discernable raised margin of callus. The outer lip in such shells is usually marked by a change in angle when viewed from the apex and is often a different color. Presumably, a strengthened lip, either internally, externally, or both, imparts adaptive value in protecting the snail from predation.

Most cystiscid genera, including "*Cystiscus*" (the group with a triserial radula), *Cystiscus* s. str., *Crithe*, *Gibberula*, and *Canalispira*, completely lack an external varix. Only the cystiscid genus *Persicula* varies in this character, with some species possessing a well-developed external varix, whereas others completely lack it. *Granulina* and *Pugnus* are the only cystiscid genera that always possess a strong external varix. Because the very strong axial costae in *Extra* resembles varices, the presence of this character is indeterminate. Based on other conchological characters, *Extra* has been placed with *Crithe* and *Cystiscus*, both non-varicose genera.

Marginellid genera, as opposed to cystiscid genera, nearly always possess a strong external varix. *Hyalina*, a notable exception, usually lacks an external varix. The genera *Prunum* and *Volvarina* vary in this character, some species possessing a strong varix, some a weak varix, and other species completely lacking it. The remaining marginellid genera always possess at least a weak external varix. This usually very strong, distinct varix often continues around the anterior edge of the siphonal canal. A few species have an extremely thickened external varix that is doubled or "duplicate."

Ontogenetic lip development, from initial formative stages in the juvenile, through subadult, to the fully adult stage, has seldom been reported in the literature. We have studied late juvenile and subadult shells for many years in an attempt to ascertain stages of labial development. The external varix is initially formed by an outward upturning of the thin lip edge in most species with a varicose adult shell. Callus deposition subsequently occurs internally and externally, resulting in the thick-

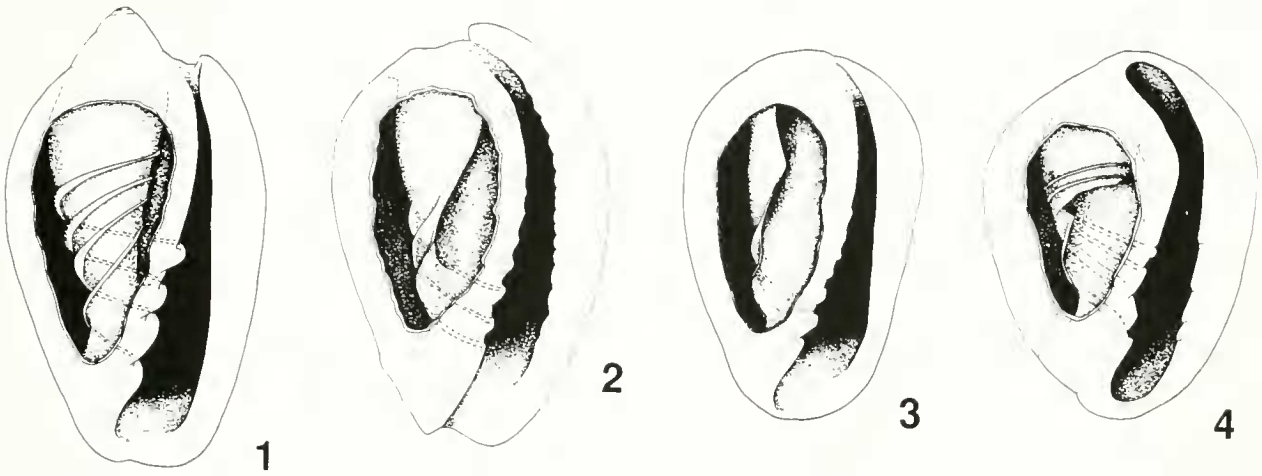
ened, adult varix. We have observed this sequence in the cystiscids *Persicula cingulata* (Dillwyn, 1817) and *P. persicula* (Linné, 1758), and in the marginellids *Eratoidea margarita* (Kiener, 1834), *Marginella rosea* Lamarck, 1822, and *Glabella adansoni* (Kiener, 1834). Because the situation in *Prunum* and *Volvarina* is more complex, we transversely sectioned, polished, and studied many shells from these genera. Preliminary results indicate that some varicose species of *Prunum*, but not *Volvarina*, form the varix as described above. This can often be seen in cross-sections, with the initial varix and subsequent concentric growth rings showing clearly. Other varicose species of both *Prunum* and *Volvarina* initially curve the thin, fragile, developing lip edge inwardly, subsequently adding further callus deposits internally to strengthen and thicken the edge. Only later are significant external callus deposits added in those species with a varicose adult shell. Preliminary results with shell cross-sections of *Prunum* and *Volvarina* indicate a difference in how this occurs. Varicose *Prunum* species with an initially incurved lip produce the varix by adding shell material to both surfaces while extending the growing edge. This can be seen in cross-section as very fine concentric growth rings centered around an initial growing point. Varicose *Volvarina* species, on the other hand, produce the varix by callus deposition internally and externally, without much elongation of the labial edge and lack obvious concentric growth rings. The same difference appears to exist between non-varicose *Prunum* and *Volvarina* species, but the external varix simply does not form in these taxa. Additional study of this character is needed before definite conclusions can be drawn, but preliminary results indicate the existence of a potentially useful taxonomic character.

Labial Denticles: Many marginelliform shells have an outer lip with distinct denticles, referred to herein as labial denticles or denticulate lip. This is preferred over such terms as "teeth," "crenulations," or "crenate." Presence or absence of labial denticles is sometimes of generic value but is usually only of specific value. Lirae are a different type of labial structure and are very useful taxonomically. They are usually erroneously referred to as "denticles" or "teeth" in the literature, but the difference is very important. Denticles are small bumps or tooth-like projections on the inside edge of the outer lip and generally do not extend into the aperture. Lirae are thin spiral ridges on the inside of the outer lip oriented perpendicularly to the lip edge and extending well inside the aperture. They resemble denticles only at the outer edge of the lip. The only marginelliforms possessing lirae (but not in all species) are the cystiscid genera *Persicula*, *Canalispira*, and *Gibberula*. These lirate genera usually lack an external varix.

Columellar Plications: Another extremely important character complex is the number and formation of columellar plications. The terms "fold," "plica," and "plait," used by other authors, are considered inappropriate for a spirally wound ridge of shell material that is deposited upon the columella and is not an actual fold of shell material. The term columellar plication is thus preferred. The anteriormost plication of marginelliform shells does not differ fundamentally from the adjacent plication, and is thus not differentiated by a separate term, such as "siphonal fold" or "basal fold." This anteriormost plication is herein considered the first plication, thus counting anterior to posterior. In many animal groups, serial features are likewise counted in a standard anterior to posterior direction. A few authors, mostly of older works, numbered plications from posterior to anterior, resulting in the anteriormost plication being variously numbered. A survey of marginelliform gastropods reveals that the first columellar plication borders the anterior edge of the columella in all cases (usually continuing and merging with the external varix) except *Afrivoluta*, which has a very volute-like columella. Two fundamentally different plicational conditions occur in marginelliform species. These are correlated with the type of internal whorls present.

Internal Whorls: One group has typical neogastropod internal whorls that are simply previous body whorls subsequently enclosed by additional whorls without further modification. The columellar plications remain unmodified for their entire length. This type of plicate internal whorl has also been observed in the families Turbinellidae, Cancellariidae, Mitridae, Costellariidae, and Volutidae. The internal whorls in true marginellids are maintained at their original thickness with no apparent resorption or further modification and are herein termed unmodified internal whorls (figure 1). Taxa with unmodified internal whorls have columellar plications remaining at their original strength and number throughout subsequent whorls. These plications can be found intact internally upon the entire length of the columella. They are here termed continuous columellar plications and are normally oriented nearly perpendicular to the shell axis. The usual number of plications in this group is four, but varies from two to six among different species, although not normally varying within a species. In those species with five or six plications, the fifth and sixth continue internally for at least a half whorl, and often are fully continuous. These are also considered continuous plications in this paper. In some species, a weak "false fifth plication" (or less commonly a "false fourth" or "false sixth") is present. This may be either a parietal lira that does not continue into the aperture for more than an eighth of a whorl, or a denticle, but neither are true plications because they are not continuous. Within marginelliform gastropods, unmodified internal whorls and continuous columellar plications are found only in species herein assigned to the Marginellidae s. str.

Another group has extremely thin, largely resorbed internal whorls, often partially missing due to complete local resorption or breakage. Proceeding inward, the first three (anterior) columellar plications in the aperture are quickly reduced to two, the third simply diminishes within a half whorl internally. The remaining two are further reduced to a single, sharp, very oblique columellar edge



Figures 1–4. Internal shell whorls. **1.** *Prunum prunum* (Gmelin, 1791), showing unmodified internal whorls. GAC, no data. Length 30.9 mm. **2.** *Persicula persicula* (Linné, 1758), showing cystiscid internal whorls. GAC Acc. # 54–87, Joal River, Senegal, on sand flats at mouth of river. Length 20.0 mm. **3.** *Plesioeystiscus jewettii* (Carpenter, 1857), showing cystiscid internal whorls. GAC Acc. # 14–90, California. Length 5.7 mm. **4.** *Granulina hadria* (Dall, 1889), showing modified cystiscid internal whorls. GAC 824, Tampa Bay, Pinellas Co., Fla., 0.3—0.6 m, shallow grass flats. Length 2.0 mm.

within one full internal revolution. This single, sharp columellar edge essentially becomes the axis of the shell. The shape of the internal whorls are very different from the original juvenile body whorls that were subsequently resorbed after being enclosed by the next whorl. Original juvenile shell color, patterns, and apertural columellar plications, generally more than two, are all completely resorbed. Among marginelliform gastropods, this type of internal whorl is found only in species here assigned to the Cystiscidae. They are here termed cystiscid internal whorls (figures 2, 3). Columellar plications in species possessing cystiscid internal whorls differ fundamentally from the continuous plications found in species with unmodified internal whorls, primarily because they are quickly reduced to a single columellar edge, and are not continuous internally. They are here termed internally reduced columellar plications. Posterior to the three internally reduced columellar plications are one to ten parietal lirae superficially resembling columellar plications. These were not differentiated from columellar plications by most previous authors. Parietal lirae are somewhat smaller and weaker than the three anterior plications, do not continue into the aperture for more than a quarter turn, and gradually diminish posteriorly. This results in a total of up to 13 "plications," of which only the anterior three are considered true, but highly modified, plications. This columellar arrangement, composed of internally reduced columellar plications plus parietal lirae, is herein termed multiplicate. This term has been used by some previous authors, but was not clearly defined. In a few cases, there may be parietal denticles posterior to the parietal lirae, but these are even shorter. A very few species of *Cystiscus* have only two columellar plications (one species, possibly not a cystiscid, is reported to have only a single plication).

A modification of the cystiscid internal whorl has been studied in species herein assigned to the genus *Granulina*. This modified type is characterized by the first two columellar plications (proceeding inwardly) abruptly ending within one full revolution internally. At this point, a thin, axially oriented edge begins much as in species with cystiscid internal whorls. However, the two posterior columellar plications continue and are situated at the anterior edge of the more bulbous portion of the mostly resorbed internal whorl. These usually translucent internal whorls are extremely thin and fragile and break very easily. The anterior end of these whorls appears to be open. We believe that this is a modification of the cystiscid internal whorl and is herein referred to as a modified cystiscid internal whorl (figure 4). The four columellar plications of *Granulina* superficially resemble continuous plications, but because the first two quickly terminate, they are considered to be internally reduced columellar plications typical of all other cystiscids. The posterior two continue, and are herein referred to as pseudo-continuous plications because they apparently do not continue for more than a whorl or two internally. Members of the genus *Granulina* lack the gradually weakening parietal lirae posterior to the columellar plications, and thus they do not have a multiplicate columella typical of other cystiscids.

Apertural Characters: The extent to which the aperture is occupied by the columellar plications is useful taxonomically. Genera with a multiplicate columella usually have more than half the apertural length occupied by the plications plus parietal lirae. *Marginella*, *Glabella*, *Dentimargo*, and *Eratoidea* have four strong, continuous columellar plications occupying more than half the apertural length, as do *Austroginella* and many of its relatives. Most remaining typical marginellids have four plications occupying less than half the apertural length.

In a few genera, though, the plications are crowded anteriorly. Columellar plications are also very useful taxonomically at the species level. In addition to the number of plications, other useful characters include their height, thickness, shape in cross-section, extent of protrusion from the aperture, their angle, whether they are fused or separate, and whether or not they are excavated inside the aperture. Very little use has been made of these features in the literature.

Another feature of the aperture is its relative width, which can often be compared to the lip thickness as a readily available reference. Most genera have an aperture that is widest anteriorly, but in some the aperture is broadest medially.

Siphonal Notch: The presence or absence of a siphonal notch is an important shell character. Called "anterior notch," "notched anterior canal," or "siphonal canal" by various authors, the term siphonal notch is preferred, as it relates to the function of this feature. A distinct siphonal notch is present in *Persicula* and *Gibberula*, but absent in the related *Canalispira*. This notch is a typical character of *Glabella* and most *Marginella* s. str. The genera *Afrivoluta* and *Marginellona* possess a siphonal notch, although it is weak in *Marginellona*. *Austroginella* has a distinct siphonal notch, but in the related *Mesoginella* the notch is very weak to absent (Coovert, 1988b). In all remaining marginelliform genera the notch is very weak or absent.

Posterior Notch: A weak to distinct posterior notch is sometimes developed at the junction or commissure between the body whorl and the posterior end of the lip. The posterior end of the lip generally forms an abrupt angle just prior to joining the body whorl, leaving a broad to narrow notch between the lip and body whorl. Less commonly, this notch forms as a weak to distinct groove in the posterior end of the lip itself. Variously termed "posterior notch," "posterior sinus," "posterior canal," "anal canal," or "anal sulcus," posterior notch is preferred, because it is consistent with "siphonal notch." The terms "anal canal" or "anal sulcus" imply a functional aspect not borne out anatomically. The presence or absence of this character is often obscure, reducing its taxonomic importance. However, many *Persicula*, *Gibberula*, and *Canalispira* have a distinct posterior notch formed at the junction of the body whorl and posterior end of the lip. The posterior notch in *Persicula* is often accentuated by an adjacent callus deposit on the body whorl. The deeply channeled, narrow notch in *Canalispira* is diagnostic. *Protoginella* has a posterior notch formed in the posterior corner of the lip itself.

Spire: Spire height is often important taxonomically. Several groups have a completely immersed spire and thus an easily recognizable shell shape. In this paper, a low spire is defined as having a length less than ¼ the shell length (figures 43, 44, 48, 55). A spire of medium height ranges from ¼ up to ⅓ the shell length (figures 57, 73), whereas a tall spire is more than ⅓ the shell length (figures 49, 70). Spire height often varies considerably within a genus and is thus more important at the species level. Spire height is determined by the insertion point of the posterior end of the lip, and can be referenced by whether or not the posterior end of the lip joins the body whorl at, above, or below the previous suture. This is a very useful character within *Volvarina*, for example.

Shape: Shell shape is another useful feature, and although somewhat subjective, should be carefully described using standard shape names. Marginelliform shells vary from a nearly round, globose outline to elliptic, obovate, obconic, conic, biconic, subtriangular, pyriform, elongate-ovate, subcylindrical, cylindrical, and other combinations. The shape of the shoulders is very important in determining overall shell shape, and can be gently curved to strongly rounded or carinate.

Size: Shell size is often very valuable as a species-level character and, in a general way, for higher categories. Shell size is here reported as minute for shells up to 2.4 mm in length, small for shells over 2.4 mm up to 6.0 mm, medium for shells over 6.0 mm up to 13.0 mm, moderately large for shells over 13.0 mm up to 25.0 mm, large for shells over 25.0 and up to 50.0 mm, and very large for shells over 50.0 mm in length.

Surface Features: Shell texture is another very useful conchological feature. Although most marginelliform shells are perfectly smooth and glossy, some have very characteristic weak to strong axial costae. This term is preferred over "axial ribs" or "longitudinal ribs." This character is often useful at the genus or the species level. Pronounced surface texture is very rare in the family, but *Pugnus* and a few *Granulina* have a minutely sculptured surface. *Rivomarginella* species have minute pustules ventrally that are part of the callus deposit. Many other species have callus deposits ranging from a thin parietal wash to distinct deposits on the spire, posterior parietal area, or anteroventrally. *Afrivoluta* has a very distinctive callus pad (Coovert, 1987a). The placement of callus deposits is species specific and thus diagnostic in the *Persicula cornea* group (Coovert, 1987b). Many *Granulina*, *Crithe*, and other species have a characteristic callus deposit here termed a collabral parietal callus ridge (figures 55, 56). This is a narrow ridge of callus deposited parallel to the lip and usually lying just outside the aperture. It often interesects the columellar plications, causing them to appear excavated. Heavier callus deposits at vulnerable points are interpreted as a protective adaptation against predatory boring. Preliminary observations suggest a strong correlation between typical bore hole locations in uncallused species and locations of callus deposits in related species.

Color: Shell color and pattern are also useful taxonomic characters. Most small species are translucent to opaque white. Most larger species are white, but some range from gray or greenish-gray, to brown, amber, flesh-colored, yellow, orange, pink, rose, or even red. The base color may be overlain with various pattern elements of

a different color. These can consist of spots, irregular blotches, spiral lines or bands, axial or oblique bands or streaks, oblique lines, or various combinations of these features.

COMPARATIVE ANATOMY OF MARGINELLIFORM GASTROPODS

External Anatomy: Features of the external anatomy of 82 species of marginelliform gastropods have been reviewed and summarized (Coovert, 1987g). Since then, a number of additional species have been reported in the literature (Coovert, 1988e:37). Our additional research, plus notes and excellent photographs of the living animals shared by others, provided a clearer picture of the external anatomy of this group. Data on 183 species are summarized in this paper. The four basic morphologic types are summarized first, along with a discussion of general features of the external anatomy. Further details of the external anatomy of each genus can be found in the systematic section.

The four distinct animal "types" delineated and summarized in Coovert (1987g) are based primarily on features of the head. The most common marginelliform animal is termed a "Type 2 animal," which has a simple, unmodified head described by some authors as "bifurcate" (figures 7, 8). The long, slender tentacles emerge from the anterior end of the head, resulting in a bifurcate appearance. Viewed from above, as most photographs are oriented, this bifurcation is not readily apparent. The long, slender tentacles have an eye located on a slight swelling at their bases. The siphon, as in all marginelliform gastropods, is a simple tube formed by the inrolled edges of an elongated expansion of the mantle edge. The siphon in Type 2 animals is moderately long to very long, and simple or weakly notched distally. A few cystiscid and most marginellid genera have a Type 2 animal, which is considered to be the generalized type.

Type 1 animals, represented by *Afrivoluta* and *Marginellona*, are characterized by a broad head with a longitudinal medial furrow or channel (figures 5, 6). This channel was described by Harasewych and Kantor (1991: 10) as a "deep tubular channel along dorsal mid-line of head," apparently formed by the ventral fusion of the tentacle bases. These same authors (op. cit., p. 13) noted that this medial channel had not been reported in *Afrivoluta*, but our careful examination of a color transparency of *Afrivoluta pringlei* (ex. W. R. Liltved) has revealed that both genera share this feature. Type 1 animals are further characterized by relatively short tentacles, a simple, moderately long siphon, and a distinct, subtriangular lateral lappet on each side of the head. A small red eye is present on each lateral lappet in *Afrivoluta*. Eyes are completely lacking in *Marginellona*.

Type 3 animals are characterized by an elongate head that is longitudinally split dorsally, with the anterior end bifurcate (figures 9, 10). This configuration could be described as either having the tentacles fused ventrally, resulting in a longitudinal dorsomedial channel, or alternatively, as having a longitudinally split head completely lacking tentacles. A detailed anatomical study is needed to clarify this situation. The siphon is either very short and not readily apparent, or completely absent. Eyes are located on the sides of the head, usually in a conspicuous bulge. Type 3 animals are represented by the genus *Cystiscus* and probably also *Crithe*.

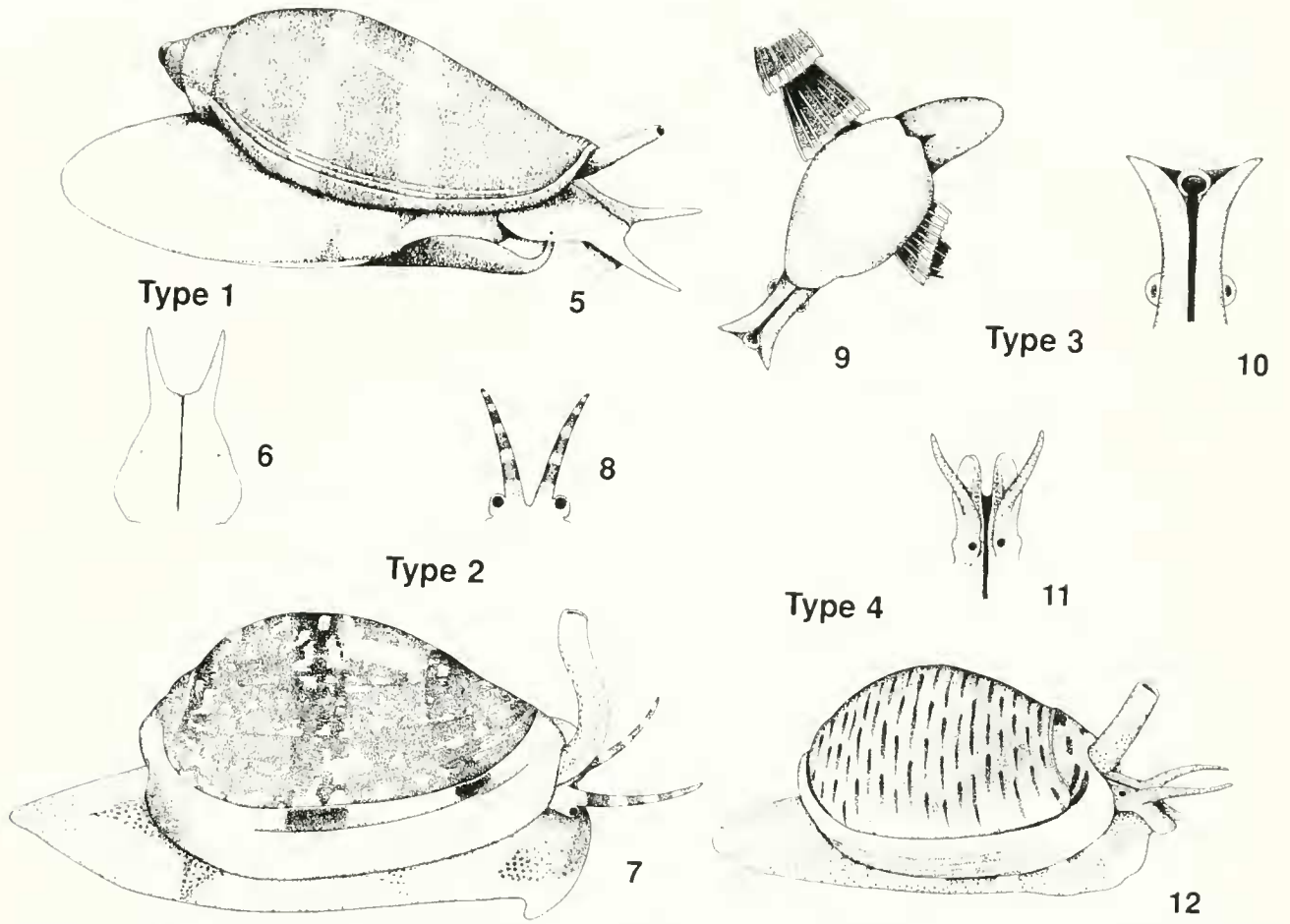
Type 4 animals have a somewhat flattened, longitudinally split head, normally with tentacles (figures 11, 12). The anterior half of the head is completely split, usually with the anterior tips pointed and divergent, but capable of closing together. These two lobes are very flexible and capable of much movement. The posterior half is only split dorsally, and fused ventrally. Tentacles, which are rarely absent, are short to long. The eyes are located on the sides of the head, slightly below the tentacle bases. The siphon is short to long, simple, and protrudes through the siphonal notch at the anterior end of the shell when the animal is active. Type 4 animals are represented by the genera *Persicula* and *Gibberula*. *Canalispira* animals differ from the typical Type 4 animal in lacking tentacles and a visible siphon (cf. Systematic section for more detail).

The siphon of most marginelliform gastropods emerges from the left side of the head, but has been described as fused to the head in *Marginellona* by Harasewych and Kantor (1991:table 3), although these authors stated that the siphon is "fused to head just left of posterior margin of mid-line channel" (op. cit., p. 10). It was described as fused to the mid-dorsal line of the head in *Prunum marginatum* by Graham (1966:135). All species studied by us (Table 3) have a siphon fused to the left side of the head. There seems to be some difference in interpretation, but probably all marginelliforms have a siphon fused to the head at least slightly left of center.

The mantle is another external anatomical feature that is useful taxonomically. Within higher taxa, the degree of mantle extension over the external shell surface varies from none to complete coverage. Extended mantles can be smooth, have low, rounded tubercles or pustules, or possess elongate papillae that are either simple or branched. The terms pustulose and papillose are used here.

Most marginelliform gastropods have a broad, flat foot, although it may be very narrow in a few species. The relative size and length of the foot may have some value taxonomically. Some species have a medially indented foot, and some (e.g. *Hyalina hyalina*, *H. pallida*, and *Prunum martini*) have an anterior, transverse pedal groove. As far as is known, females have a medial, anteroventral pedal gland on the sole of the foot. In some *Gibberula* species, the anterolateral edges of the foot are raised and laterally rolled, forming what Gofas and Fernandes (1988:22) described as "parapodia." All these characters may have taxonomic value and need further study.

Animal coloration is very useful at the species level, but has limited value for higher classification. Gofas and Fernandes (1988) and Gofas (1989a, 1990, 1992) provid-



Figures 5–8. Marginellid external anatomy. **5, 6.** *Afrivoluta pringlei* Tomlin, 1947, example of Type 1 animal. After Liltved (1985) plus pers. obs. of photos (ex. W. R. Liltved). Off Danger Point, western Cape Province, at 246 m. Ca. X 0.65. **5.** Animal viewed from right side. **6.** Dorsal view of head. **7, 8.** *Prunum aff. aletes* Roth, 1978, example of Type 2 animal. GAC 1518, small island just off Tamarindo Beach, S. of Tamarindo Diria Hotel, Guanacaste Province, Costa Rica, under rocks, low tide. Shell length 19.4 mm. **7.** Animal viewed from right side. **8.** Dorsal view of head. **Figures 9–12.** Cystiscid external anatomy. **9, 10.** *Cystiscus minutissimus* (Tenison-Woods, 1876), example of Type 3 animal. After Murray (1970) and Coleman (1975). **9.** Animal viewed from above. Ca. 9.0 X. **10.** Dorsal view of head Ca.18 X. **11, 12.** *Persicula interruptolineata* (Megerle von Mühlfeld, 1816), example of Type 4 animal. GAC 1581, N. end of Playa La Galera, Isla de Margarita, Venezuela, NE side of bay, hand-dredged on sandy mud with small patches of Turtle Grass. Length 14.7 mm. **11.** Dorsal view of head. **12.** Animal viewed from right side.

ed color plates of live animals, making excellent use of coloration or "polychromatism" for species differentiation.

Radula: The radulae of very few species (20 *fide* Coovert, 1989b) were known at the time of the last generic revision of this group (Coan, 1965). Much additional radular information has been subsequently published (see Coovert, 1989b for summary; Coovert and Coovert, 1990). This published data, combined with our unpublished data and observations of SEMs (ex. Dean Hewish), brings the number of species studied to 190. An additional 30 species are known to be non-radulate. Of the 31 Recent genera recognized in this revision, the radulae of only two are unknown.

Three basic radular patterns of marginelliform gastropods have long been recognized by the senior author. In addition to non-radulate species, the radulate species fall into two different groups. One group has a relatively long, narrow radula, the other group has a shorter, wider radula. The most fundamental differences between these two groups were not apparent until recently. In fact, Coovert (1989b:31) erroneously assigned the genera allied to *Austroginella* to the long, narrow radulate group based solely on radular width.

The first major difference noted between these two groups was the discovery of paired, wing-like extensions of the subradular membrane, found only in species with a long, narrow radula (and not in genera allied to *Austroginella*). These structures, which persist in routine maceration with KOH, were first noticed by Dean Hewish (pers. comm.), and later confirmed by us in a number of species. They were originally called "membranous wings," and appeared to be attached anteriorly to the

radular ribbon at the bending plane. They are not readily visible after permanent mounting on microscope slides.

We follow Coan (1965) in useage of the term rachidian plate rather than "rachidian teeth" because of the wide, multicusped nature of these structures in marginelliform radulae.

We discovered that two different conditions of rachidian plate development occur on the posterior end of the radula where plates are initially secreted. Species with a long, narrow radula have a series of at least 6, and up to 12 or more, gradually formed rachidian plates at the posterior end, which are enclosed in a radular sac. These plates, initially narrower and rudimentary, are extremely thin, clear, and very difficult to discern in slide preparations. Progressing anteriorly, these plates become wider and more visible, first developing medially, with lateral portions forming next, finally followed by full cusp development. We refer to these separate undeveloped plates as nascent rachidian plates, and the gradually developing series as a developmental series. Just anterior to the nascent plates, a series of up to 40 or more fully formed plates are distinctly brown-tinged, followed by fully developed, clear, normal-appearing plates. In contrast, species with a short, wide radula have only one or two nascent plates posteriorly. These plates are fully formed with completely developed cusps, but are extremely thin, clear, and often very difficult to discern in microscope slide preparations. The first plate often appears as a "ghost image." We term these preformed nascent rachidian plates. Just anterior to these nascent plates, a series of 4 to 5 fully formed brown-tinged plates are followed by fully developed, clear, normal-appearing plates. The buccal pouch, characteristic of marginellids in the strict sense (see Internal Anatomy section), contains the posterior end of the radula in this group. Thus, two fundamentally different conditions exist in both overall structure and development of the posterior end of marginelliform gastropod radulae.

In our search for taxonomic characters of marginelliform radulae, we noted that Ponder (1970:70) reported two completely separate odontophoral cartilages in *Gibberula* (as *Diluculum* sp.). A pair of anteriorly fused odontophoral cartilages (described as a single cartilage in *Volvarina taeniolata*, see Fretter, 1976:329) were described from all other studied species. None have been illustrated. We dissected *Persicula interruptolineata* (Megerle von Mühlfeld, 1816), a close relative of *Gibberula*, to confirm the presence of separate odontophoral cartilages. Rather than underlying the radular ribbon as in typical marginellids, the two separate odontophoral cartilages of *Persicula* each fit into one of the "membranous wings" that flank the radular ribbon (figures 15, 16). Further work determined the shape and attachments of these wing-like membranous structures. These paired, hood-like extensions of the subradular membrane (more accurately termed the cuticle, see Hyman, 1967:236), which serve to receive the odontophoral cartilages, are here referred to as odontophoral cartilage hoods (figures 13–16). Nothing resembling these structures has been reported in marginellids with a short, wide radula. A radula from a specimen of *Prunum aff. aletes* Roth, 1978, which was not macerated in KOH, revealed anterolateral extensions of the radular ribbon cuticle. These, however, were narrower lateral flanges that differ functionally from the odontophoral cartilage hoods of *Persicula*. These extensions of the cuticle apparently help hold the radular ribbon in correct alignment with the underlying odontophoral cartilage. We term these structures marginal cuticular flanges (figures 17–20). Unlike odontophoral cartilage hoods, they are lost during routine maceration

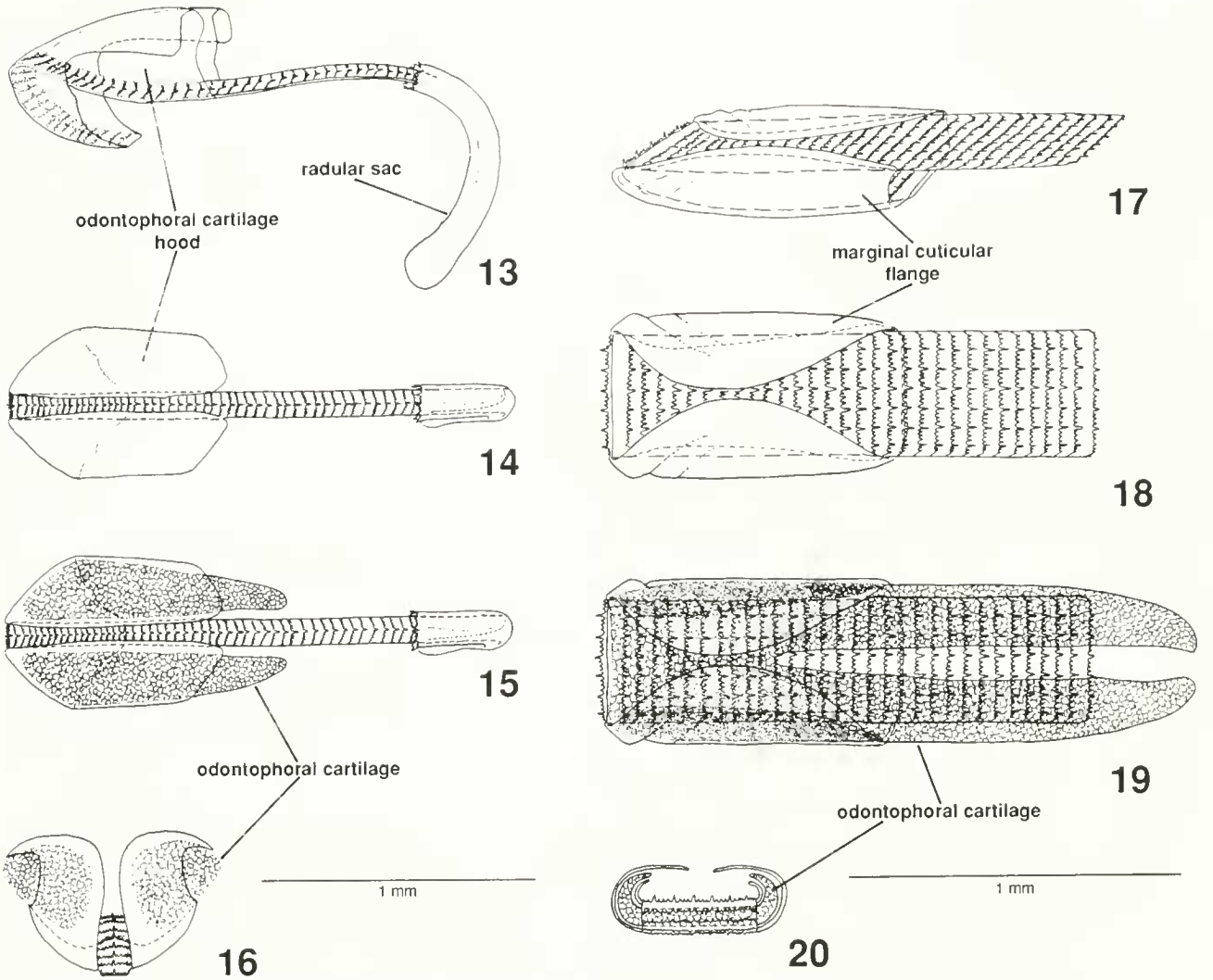
Table 2. Anatomical character states utilized in Table 3

1. Buccal pouch	0—absent 1—present
2. Neogastropod radular sac	0—present 1—absent
3. General radular type	0—cystiscid 1—marginellid 2—absent
4. Specific radular type	0—absent 3—Type 3 radula 5—Type 5 radula 6—Type 6 radula 6m—modified Type 6 radula 7—Type 7 radula
5. Odontophoral cartilages	0—separate 1—anteriorly fused 2—fused both anteriorly and posteriorly 3—absent
6. Siphon	0—attached left of head 1—fused to head
7. Valve of Leiblein	0—present, no bypass tube 1—present, with bypass tube 2—absent
8. Esophageal caecum	0—absent 1—present
9. Gland of Leiblein	0—small, narrow gland, no terminal bulb 1—large, saceulate gland, no terminal bulb 2—with terminal bulb and long, convoluted duct
10. Duct of gland of Leiblein	0—empties into esophagus posterior to nerve ring 1—passes through nerve ring, emptying into anterior end of proboscis either into buccal cavity or anterior end of anterior esophagus
11. Paired salivary glands	0—ascinous 1—tubular
12. Paired salivary gland attachment	0—attached to esophagus 1—free of esophagus
13. Paired salivary glands, ducts	0—embedded in walls of esophagus 1—attached to esophagus 2—free of esophagus
14. Accessory salivary glands	0—absent 1—single gland present

Table 3. Summary of anatomical features of marginelliform gastropods. Character states given in Table 2. Sources of data given in Table 4. ? indicates character state unknown or uncertain.

Character states

Cystiscidae	1 Buccal pouch 0-absent, 1-present	2 Neogastropod radular sac 0-present, 1-absent	3 General Radular Type 0-cystiscid, 1-marginellid, 2-absent	4 Specific Radular Type 0-absent, Types 3, 5, 6, 6m, 7	5 Odontophoral cartilages 0-sep., 1-ant. fused, 2-both fused, 3 abs	6 Siphon 0-left of head, 1-fused to head	7 Valve of Leiblein 0-pres no bypass, 1-pres w/bypa, 2- abs	8 Esophageal caecum 0-absent, 1-present	9 Gland of Leiblein 0-sm, narr., 1-lg, sacc., 2-w/term. bulb	10 Duct of gland of Leiblein 0-post. to nerve rng., 1-thru nerve rng	11 Paired salivary glands 0-acinous, 1-tubular	12 Paired salivary gland attachm 0-attach. to esophagus, 1-free of esoph.	13 Paired salivary glands, ducts 0-embed. in esoph., 1-attach. to, 2-free	14 Access. salivary glands 0-abs., 1-single gland pres
Persicula interruptolineata	0	0	0	3	0	0	0	0	0	0	0	0	1	1
Persicula masirana	0	0	0	3	0	0	0	0	0	0	0	0	1	1
Gibberula sp.	0	0	0	3	0	0	1	0	0	0	1	0	0?	1
Marginellidae														
Marginellona gigas	1	1	1	7	?	1	0	0	1	0	1	1	2	0
Serrata mustelina	1	1	1	6m	1	0	1	0	2	0	1	0	0	1
Austroginella johnstoni	1	1	1	5	1	?	1	0	2	0	1	0	0	0
Austroginella muscaria	1	1	1	5	1	?	1	0	2	0	1	0	0	0
Mesoginella pygmaea	1	1	1	5	1	0	1	0	2	0	1	0	0	0
Volvarina avena	1	1	1	6	2	0	2	1	2	1	0	1	1	1
Volvarina taeniolata	1	1	1	6	2	?	2	1	2	1	0	1	2	1
Prunum aletes	1	1	1	6	1	0	2	1	2	1	1	1	2	0
Prunum guttatum	1	1	1	6	1	0	2	1	2	1	0	1	1	0
Prunum marginatum	1	1	1	6	?	1	2	1	2	1	0	1	2	0
Prunum martini	1	1	1	6	?	0	2	1	2	1	1	1	2	0
Prunum prunum	1	1	1	6	2	0	2	1	2	1	1	1	1	1
Prunum roosevelti	1	1	1	6	2	0	2	1	2	1	1	1	2	0
Bullata bullata	1	1	1	6	?	0	2	1	2	1	?	?	?	?
Hyalina hyalina	0	1	2	0	3	0	?	?	2?	1?	1	?	?	?
Hyalina pallida	0	1	2	0	3	0	2	1	2	1	1?	1	2	1
Dentimargo cairoma	0	1	2	0	3	0	2	0	2	1	1	1	2	1
Dentimargo eburneola	0	1	2	0	3	0	2	0	2	1	0	1	2	1
Marginella desjardini	0	1	2	0	3	0	2	0	2	1	?	1	?	1
Marginella glabella	0	1	2	0	3	0	2	0	2	1	1	1	2	1
Marginella sebastiani	0	1	2	0	3	0	2	0	2	1	1	1	2	1

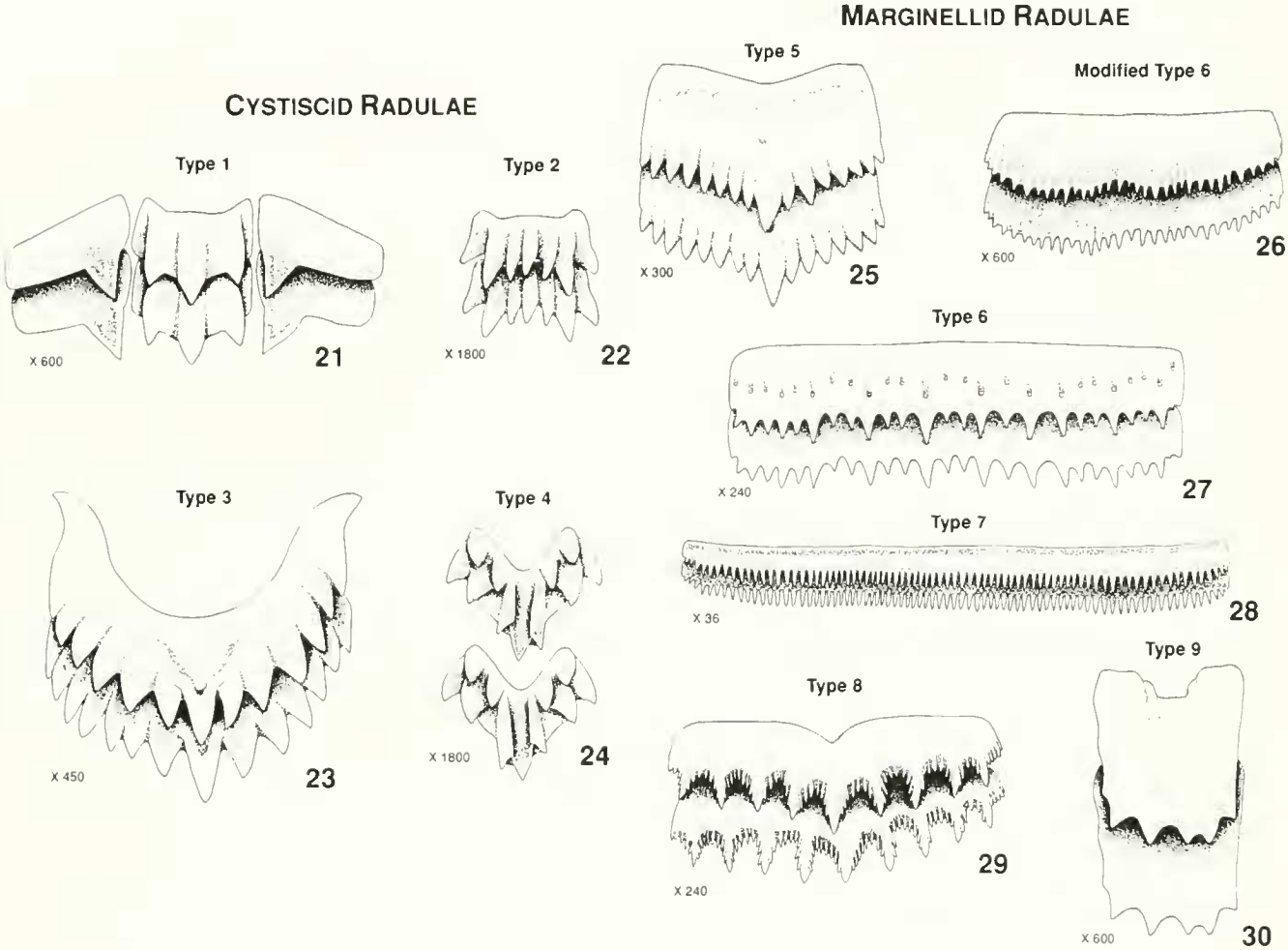


Figures 13–16. *Persicula interruptolineata* (Megerle von Mühlfeld, 1816), showing details of cystiscid radular morphology. GAC 1581, data in Table 1. Rachidian width enlarged 150% for clarity. **13.** Left lateral view, odontophoral cartilages removed, only posterior end of radular sheath shown. **14.** Same, dorsal view. **15.** Dorsal view, odontophoral cartilages in place, muscles and connective tissue removed. **16.** Same, anterior view. **Figures 17–20.** *Prunum aff. aletes* Roth, 1978, showing details of marginellid radular morphology. GAC 1518, data in Table 1. **17.** Left lateral view, odontophoral cartilage removed. **18.** Same, dorsal view. **19.** Dorsal view, odontophoral cartilage in place, muscles and connective tissue removed. **20.** Same, anterior view.

in KOH, suggesting additional differences in composition.

Morphological evidence suggests that there are two fundamentally different types of radulae. The first type has a very long, triserial or uniserial, C-shaped radula, composed of 80 to 200 or more very narrow, usually overlapping, arched rachidian plates, with relatively few (3 to 15) cusps. This type of radula has a pair of odontophoral cartilage hoods, each receiving a separate odontophoral cartilage, which flank the radular ribbon anteriorly. The posterior end of the radula begins as a developmental series of nascent plates and is enclosed in a typical neogastropod radular sac. This type of radula is found in all species here assigned to the Cystiscidae and is termed a cystiscid radula (figures 13–16). The second type has a uniserial, J-shaped ribbon composed of 10 to 80 broad, overlapping, flat rachidian plates, usually with numerous cusps (9 to 80, rarely 4 to 7). This type of radula has marginal cuticular flanges, and the odontophoral cartilages are fused anteriorly into a single structure underlying the radular ribbon. The posterior end of this type of radula starts with 1 or 2 preformed nascent rachidian plates and is enclosed in a marginellid buccal pouch. This second type is found in all radulate species here assigned to the Marginellidae s. str., and is termed a marginellid radula (figures 17–20).

Coovert (1989b:31–33) divided marginelliform radulae into seven distinct types based on characters of the rachidian plates and the presence or absence of lateral teeth. In addition to these seven types, which are discussed below, two new types are recognized. The orientation of rachidian plates refers to the large, dorsal



Figures 21–24. Cystiseid radular types. **21.** *Plesiocystiscus jewettii* (Carpenter, 1857), example of Type 1 radula. GAC radula no. 093, Pirates Cove, San Luis Obispo, California, intertidal. Ex. M1823, shell length 4.9 mm. **22.** *Cystiscus angasi* (Crosse, 1870), example of Type 2 radula. Hewish radula U, Lonsdale Bight, Victoria, Australia. Ex. NMV F53748, shell length 1.7 mm. **23.** *Persicula persicula* (Linné, 1758), example of Type 3 radula. GAC radula no. 183, Niodior, Senegal Ex. AMNH 173759, shell length 19.8 mm. **24.** *Granulina hadria* (Dall, 1889), example of Type 4 radula. GAC radula no. 038, Tampa Bay, Pinellas Co., Florida, sand and mud. Ex. GAC Acc. # 27–82, shell length 2.2 mm. **Figures 25–30.** Marginellid radular types. **25.** *Austroginella muscaria* (Lamarck, 1822), example of Type 5 radula. GAC radula no. 181, Lakes Entrance, Victoria, Australia. Ex. DMNH 12435, shell length 13.3 mm. **26.** *Serrata translata* (Redfield, 1870), example of Modified Type 6 radula. GAC radula no. 304, Raiatea, French Polynesia Ex. GAC Acc. # 2–91, shell length 4.3 mm. **27.** *Prunum apicinum* (Menke, 1828), example of Type 6 radula. GAC radula no. 147, Sunshine Key, Florida Keys, Monroe Co., Florida. Ex. Peggy Williams colln., shell length 9.5 mm. **28.** *Marginellona gigas* (Martens, 1904), example of Type 7 radula. After Thiele (1904 pl. 9, fig. 64). Ex. Holotype, shell length 80—100 mm. **29.** *Serrataginella spryi* (Clover, 1974), example of Type 8 radula. GAC radula no. 305, off Nacala Bay, N Mozambique, dredged in 20–30 m, sand Ex. GAC Acc. # 6–93, shell length 8.0 mm. **30.** *Hydroginella tridentata* (Tate, 1878), example of Type 9 radula GAC radula no. 306, Margaret River, Western Australia, in sand, 4.6 m. Ex. GAC Acc. # 13–90, shell length 7.8 mm.

section of the ribbon, not the ventrally folded anterior end. This orientation is such that the cutting edge of each rachidian plate is posterior, and the basal edge, where the plate is attached to the membrane, is anterior.

Type 1 through Type 4 radulae are all cystiseid radulae, possessing the characteristics previously defined.

Type 1 ("Triserial Type") radulae (figure 21) are triserial, with simple, thin, weak, lateral teeth that narrow to a single, posteriorly-pointed cusp. The long, narrow radula is composed of 66 to 103 rows of overlapping rachidian plates. These plates are very narrow, weakly arched, with 3 to 7 sharp cusps along cutting edge. The basal edge of each rachidian plate is slightly concave, resulting in a weakly U-shaped plate. Odontophoral cartilage hoods were noted by us as well as by Dean Hewish (pers. comm.), but the nature of the odontophoral cartilages is unknown. The genus previously referred to as "*Cystiscus*" (Coovert, 1989b), described herein as new, is the only one to possess a Type 1 radula (radulae of 3 species studied).

Type 2 radulae (figure 22) are uniserial, consisting of a

long, narrow series of over 80 to 220 rachidian plates. These plates are overlapping (rarely separate), very narrow, weakly to strongly arched, with 4 to 15 very strong cusps along cutting edge. The basal edge of each plate is slightly concave, nearly straight, or convex medially, resulting in a crescent-shaped, subrectangular, or asymmetrically V-shaped plate. Odontophoral cartilage hoods were noted in many species of *Cystiscus*, but were unknown and unobserved at the time *Crithe* radulae were extracted. The nature of the odontophoral cartilages is unknown. *Cystiscus* (radulae of 14 species studied) and *Crithe* (radulae of 1 species studied) both have a Type 2 ("*Crithe* / *Cystiscus* Type") radula. The radula of *Extra* is unknown, but presumed to be similar.

Type 3 radulae (figure 23) are uniserial, consisting of a long, narrow series of over 80 to 209 rachidian plates. These moderately to strongly overlapping plates are narrow, moderately to strongly arched, with 5 to 14 sharp cusps along cutting edge. The central cusp is often the strongest. The basal edge of each plate is strongly concave, resulting in a U- or V-shaped plate. The reports of wishbone-shaped rachidian plates (Barnard, 1962:14–15; Ponder, 1970:70; Ponder, 1973:fig. 2) are inaccurate and due to an artifact of observation (see discussion in Coovert, 1989b:12–13). Odontophoral cartilage hoods were noted in all three included genera, with a pair of separate odontophoral cartilages noted in *Persicula* and *Gibberula*. *Persicula* (radulae of 14 species studied), *Gibberula* (radulae of 21 species studied), and *Canalispira* (radulae of 2 species studied) all have a Type 3 ("*Persicula* Type") radula.

Type 4 radulae (figure 24) are uniserial, consisting of a long, narrow series of at least 90 to 159 rachidian plates. These usually completely non-overlapping plates are narrow, moderately arched, with 9 to 12 clustered, raised denticles located in staggered positions on the dorsal surface, with a single (or asymmetrically paired) strong central cusp protruding on the cutting edge. The basal edge of each plate is weakly concave, resulting in a weakly V-shaped plate. The rachidian plates are asymmetrical and alternate as mirror images (figure 24). Although odontophoral cartilage hoods have not been observed in representatives of this group, their radulae are otherwise typically cystiscid. A broad, membranous flange on either side and extending the whole length of the radula, effectively doubling the width, has been observed (Dean Hewish, pers. comm.) when using the enzyme Pronase for maceration. This is a less destructive method than the use of KOH. This flange is certainly homologous to odontophoral cartilage hoods, but the nature of the odontophoral cartilages is unknown. No further anatomical information is available. *Granulina* (radulae of 12 species studied) and *Pugnus* (radulae of 2 species studied) both have a Type 4 ("*Granulina* Type") radula.

Type 5 through Type 9 radulae are all marginellid radulae, possessing the characteristics as previously defined.

Type 5 radulae (figure 25) are uniserial, consisting of a relatively short, broad ribbon of 19 to 75 rachidian plates. These usually overlapping plates are moderately wide, weakly arched, with 8 to 22 strong cusps along cutting edge. The central cusp is often the strongest. There are often pits on adjacent plates to receive the tips of some of the cusps, especially the central. The basal edge of each rachidian plate is generally slightly concave, resulting in a rectangular to chevron-shaped plate. The odontophoral cartilages in *Mesoginella* and *Austrogiella* were described as fused anteriorly (Ponder, 1970: 62; Ponder & Taylor, 1992:320), but no detailed data exists as to marginal cuticular flanges. *Protoginella* (radula of 1 species studied), *Alaginella* (radulae of 9 species studied), *Austroginella* (radulae of 5 species studied), *Mesoginella* (radulae of 16 species studied), *Ovaginella* (radulae of 2 species studied), and *Balanetta* (radula of 1 species studied) all have a Type 5 ("*Austroginella* / *Mesoginella* Type") radula. The radula of *Closia* is unknown, but presumed to be similar.

Type 6 radulae (figure 27) are uniserial, consisting of a relatively short, broad ribbon of 24 to 75 overlapping rachidian plates. These plates are broad, nearly flat, with 9 to 45 (exceptionally 5) sharp cusps along cutting edge. There are often pits on adjacent plates to receive the tips of some or all of the cusps. The basal edge of each plate is generally straight, resulting in an elongate, rectangular "comb-like" plate. The odontophoral cartilages are fused anteriorly. They are fused posteriorly in most species (but not in *Prunum aff. aletes* and *P. guttatum*), leaving a narrow, medial, longitudinal posterior slit in most *Prunum* and *Volvarina* (figures 38–42). (See following section on internal anatomy.) A single cartilage was described for *Volvarina taeniolata* (cf. Fretter, 1976:329). The marginal cuticular flanges of *Prunum aff. aletes*, described above, are very similar in other species of *Prunum* we examined. *Prunum* (radulae of 23 species studied), *Volvarina* (radulae of 42 species studied), *Rivomarginella* (radulae of 2 species studied), *Bullata* (radula of 1 species studied), and *Cryptospira* (radulae of 4 species studied) all have a Type 6 ("*Prunum* / *Volvarina* Type") radula. Most of these are discussed and figured in Coovert and Coovert (1990).

Modified Type 6 radulae (figure 26) are similar to typical Type 6, but differ in having a shorter ribbon composed of only 13 to 35 plates, averaging more cusps (22 to 59) that project from a somewhat sinuous posterior edge, and in often having thinner and more fragile rachidian plates. Pits on adjacent plates to receive cusp tips were not observed as in many typical Type 6 radulae. The odontophoral cartilages of *Serrata* (as *Haloginella*) were described by Ponder (1970:66) as fused except for a very short posterior portion. Marginal cuticular flanges are unknown. *Serrata* (radulae of 8 species studied) is the only genus to have a Modified Type 6 ("*Serrata* Type") radula.

Type 7 radulae (figure 28) are uniserial, consisting of a relatively short, very broad ribbon of 56 to 80 overlapping rachidian plates. These plates are very broad, nearly

flat, with numerous (58 to 85) sharp cusps along cutting edge. The basal edge of each plate is generally straight, resulting in an elongate, rectangular "comb-like" plate. Odontophoral cartilages and marginal cuticular flanges are unknown. The monotypic genera *Marginellona* and *Afrivoluta* both have a Type 7 ("*Afrivoluta* Type") radula.

Type 8 radulae (figure 29), here described, are uniserial, consisting of a relatively short, broad ribbon of 38 overlapping rachidian plates. These plates are broad, nearly flat, with 9 to 10 sharp cusps on the cutting edge. The entire posterior edge, including all edges of the main cusps, with numerous (total of ca. 70) small, secondary cusps, giving the main cusps a serrated appearance. Pits for reception of adjacent cusp tips were not observed. The basal edge of each plate is slightly indented medially, resulting in a very shallowly V-shaped plate. Odontophoral cartilages and marginal cuticular flanges are unknown. The Type 8 ("*Serrataginella* Type") radula is unlike any others known, and is represented by "*Marginella*" *spryi* Clover, 1974, type species of a monotypic genus herein described as new.

Type 9 radulae (figure 30), first described by Bouchet (1989:79, fig. 3), are uniserial, consisting of a very short, narrow, greatly reduced ribbon of 10 to 30 rachidian plates. These weak plates overlap and are nearly flat, with 4 to 7 cusps on the cutting edge. Pits for reception of adjacent cusp tips are absent. The basal edge of each plate is straight, resulting in a subquadrate plate. Odontophoral cartilages and marginal cuticular flanges are unknown. *Hydroginella* (radulae of 4 species studied) is the only genus to have a Type 9 ("*Hydroginella* Type") radula. One species is known to be parasitically associated with fishes (Bouchet, 1989). Judging from the very similar radulae of other species, it seems likely that all may have such an association.

A third major group, comprised of non-radulate species, completely lacks a buccal mass, odontophore, and radula. This was confirmed by dissections of species in the following genera: *Dentimargo* (Ponder, 1970:67, plus species reported herein), *Marginella* s. str. (Graham, 1966: 139, Coan & Roth, 1976:220, plus species reported herein), *Glabella* (Coan & Roth, 1976:220), and *Hyalina* (Coan & Roth, 1976:220, and herein). Other species have been subsequently reported to lack a radula, some based on unsuccessful radular extraction with KOH (see Coovert, 1989b for review). Thus, a total of 31 species have been inferred or demonstrated to lack a radula. We have attempted routine radular extraction on separate occasions from two specimens of the type species of *Eratoidea*, *E. margarita* (Kiener, 1834), and have not found a radula. Although not definitive, it is suggested that this genus is also non-radulate. This assemblage of non-radulate genera is an artificial group, with *Hyalina* belonging to a different lineage (see discussion in systematic section).

Internal Anatomy: Prior to our studies, only 13 species of marginelliform gastropods had been studied anatomically. Harasewych and Kantor (1991:tables 2, 3) summarized anatomical data of the 11 species known at that time. Ponder and Taylor (1992) subsequently presented data for two species of *Austroginella*. Few taxonomic conclusions could be drawn from such a relatively small sample because the anatomy varied so greatly. Our dissections added anatomical data for 11 additional species, and further data for one previously reported species (Tables 1–4). Combined with conchological and radular data, this greatly expanded body of anatomical information enabled taxonomic groupings to become evident, making a reliable and stable classification possible. Details of the foregut were emphasized because of their greater taxonomic value. Our primary objective is a presentation of the higher classification, therefore, more detailed reports on the anatomy of individual species will be published elsewhere. A discussion of foregut anatomy follows, along with a summary of known anatomical information for these 24 species.

The proboscis of marginelliform gastropods is relatively short and pleurembolic. The retractor muscles are inserted on the sides of the proboscis, resulting in the basal portion being invaginated, forming a proboscis sac (Fretter & Graham, 1962:150). The proboscis varies somewhat in shape among genera. The small mouth is always situated terminally at the anterior end. Most genera have a proboscis that is rounded or blunt distally, and, when retracted, is generally about two-and-one-half to four times as long as broad. When feeding, the proboscis may be extended to a length approximating the length of the shell in at least some species (Fretter, 1976: 329). Both species of *Dentimargo* studied have a distally pointed proboscis about four times as long as broad when retracted (figure 33). *Serrata aff. mustelina* has a more bulbous, distally rounded proboscis about one-and-a-half times as long as broad. *Gibberula* and *Persicula* (figures 35, 79) both have a short, broad proboscis about two times as long as broad.

The mouth opens directly into the buccal cavity. No jaws have been observed in any marginelliform species. In radulate species, the buccal cavity leads posterodorsally to the anterior esophagus and posteroventrally to the buccal mass. In non-radulate species, the buccal cavity leads with little or no differentiation to the anterior esophagus.

The most significant hallmark of the family Marginellidae, in the strict sense, is the possession of a "buccal pouch" or "buccal caecum" in radulate species. Both Fretter (1976:333) and Harasewych and Kantor (1991: 16) recognized the significance of this structure and its presence only in marginellids and toxoglossans. The buccal pouch (figure 31), the term we prefer for this structure, was first discovered and named by Graham (1966: 137), who noted that "in marginellids the most interesting feature of the gut is the situation of the buccal mass, wholly withdrawn into a caecum from its typical place on the floor of the buccal cavity (op. cit., p. 147)." The buccal mass, described as "rather reduced" by Graham (1966:137) and consisting of the odontophoral cartilages,

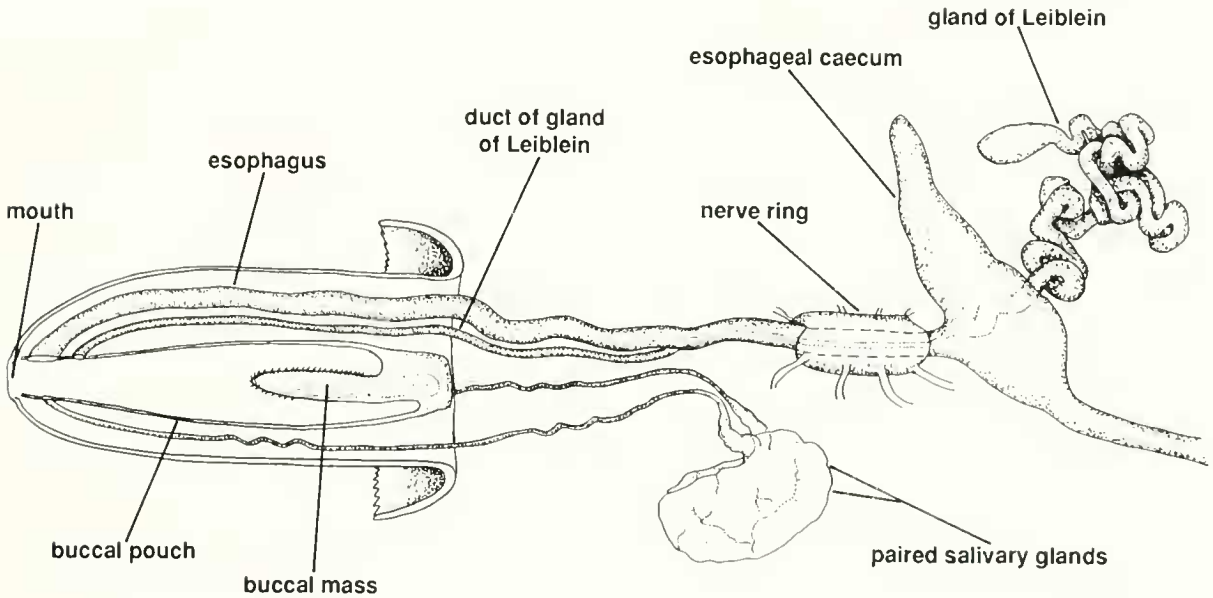
Table 4. Sources of anatomical data utilized in Table 3

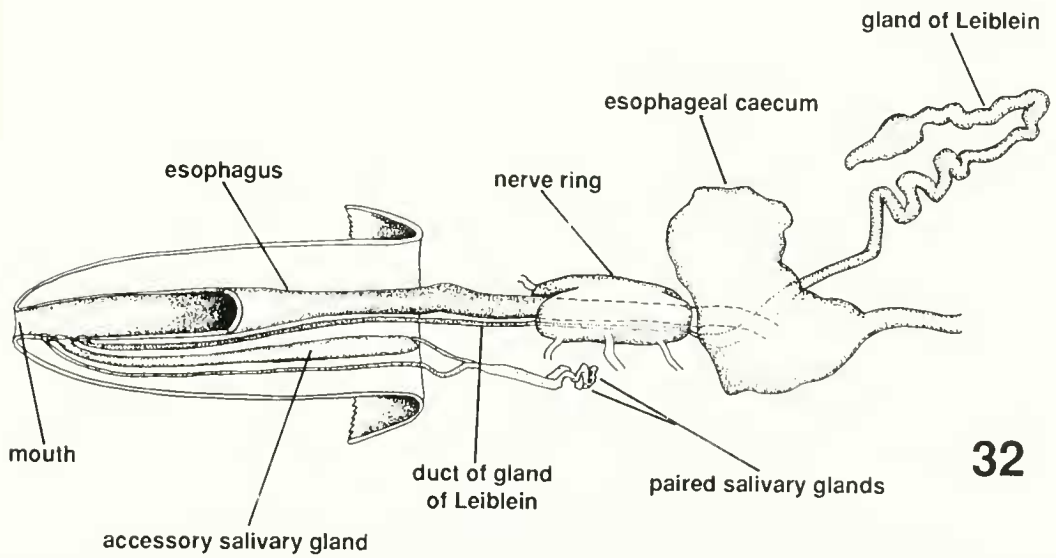
Species (current nomenclature)	Source
Cystiscidae	
Persicula interruptolineata (Megerle von Mühlfeld, 1816)	herein; see Table 1 for data
Persicula masirana Roth & Petit, 1972	herein; see Table 1 for data
Gibberula sp.	Ponder (1970), as *Diluculum* sp.
Marginellidae	
Marginellona gigas (Martens, 1904)	Harasewych and Kantor (1991)
Serrata aff. *mustelina* (Angas, 1871)	Ponder (1970), as *Volvarina* (*Haloginella*) *mustelina*; the New Zealand species differs from the Australian species; see Coovert (1989b:16) for comments
Austroginella johnstoni (Petterd, 1884)	Ponder and Taylor (1992)
Austroginella muscaria (Lamarck, 1822)	Ponder and Taylor (1992)
Mesoginella pygmaea (G. B. Sowerby II, 1846)	Ponder (1970), as *Mesoginella* (*Sinuginella*) *pygmaea*
Volvarina aff. *avena* (Kiener, 1834)	herein; see Table 1 for data
Volvarina taeniolata Mörch, 1860	Fretter (1976)
Prunum aff. *aletes* Roth, 1978	herein; see Table 1 for data
Prunum guttatum (Dillwyn, 1817)	herein; see Table 1 for data
Prunum marginatum (Born, 1778)	Graham (1966), as *Marginella mariginata*
Prunum martini (Petit, 1853)	Marcus and Marcus (1968), as *Mariginella fraterculus*
Prunum prunum (Gmelin, 1791)	herein; see Table 1 for data
Prunum roosevelti (Bartsch & Rehder, 1939)	herein; see Table 1 for data
Bullata bullata (Born, 1778)	herein; see Table 1 for data
Hyalina hyalina (Thiele, 1913)	Eales (1923), as *Marignella hyalina*
Hyalina pallida (Linné, 1758)	Coan and Roth (1976) plus herein; see Table 1 for data
Dentimargo cairoma (Brookes, 1924)	Ponder (1970), as *Volvarinella cairoma*
Dentimargo eburneola (Conrad, 1834)	herein; see Table 1 for data
Marginella desjardini Marche-Marchad, 1957	Graham (1966)
Marginella glabella (Linné, 1758)	herein; see Table 1 for data
Marginella sebastiani Marche-Marchad & Rosso, 1979	herein; see Table 1 for data

radula, and associated connective tissue and muscles, is contained in the buccal pouch. What characterizes the buccal pouch is the sphincter at its anterior opening into the buccal cavity and the fact that it is a separate caecum or sac that is blind posteriorly, where the radula is initially secreted. This is further discussed by Graham (1966: 138), who noted that radular formation occurs "at the innermost end of the pouch, which therefore corresponds to the radular sac of more normal gastropods." Ponder (1970:76) also noted that the buccal pouch is derived from the radular sac. Fretter (1976:329) observed that the "teeth arise at the innermost end of the pouch where there is no clear demarcation of the radular sac typical of prosobranchs." The blind end of a buccal pouch thus corresponds to the posterior end of the radular sac. Our observations of *Prunum*, *Volvarina*, and *Bullata* species confirmed the presence of a buccal pouch. The genera *Serrata*, *Mesoginella*, and *Austroginella*, dissected by Ponder (1970) and Ponder and Taylor (1992), likewise possess a true marginellid buccal pouch. In the true marginellids, the odontophore extends beyond the posterior end of the radula.

The absence of a buccal pouch in non-radulate species has been confirmed by dissections of species of *Hyalina*, *Dentimargo*, and *Marginella* (figures 32–34). Graham (1966:139) described what he believed to be a vestigial buccal pouch in *Marginella desjardini*. Ponder (1970: 76) considered this to be the accessory salivary gland. Our dissections of *Marginella glabella* (figure 34) and *M. sebastiani*, both close relatives of *M. desjardini*, confirmed this contention, because an accessory salivary gland was found in both species, but neither had a vestigial buccal pouch. Ponder's (1970: fig. 3B) dissection of *Dentimargo cairoma*, and our dissection of *D. eburneola* (figure 33), show the complete absence of a buccal pouch. There is insufficient information about *Hyalina hyalina* in Eales (1923) to draw any conclusions. Coan and Roth (1976:220) likewise did not provide sufficient detail for *H. pallida*, although they did mention the absence of a radula and odontophore. Our dissection of *H. pallida* (figure 32), confirms the absence of a buccal pouch.

A typical neogastropod radular sac enclosing the posterior end of the radula was found in both species of *Persicula* we dissected (figure 35). In *Persicula interruptolineata* and in the *Gibberula* studied by Ponder (1970:fig. E, r.s.), the radular sac is readily distinguished because it protrudes from the posterior end of the proboscis in a characteristic downward curve (figures 35, 79). It is further characterized by a slightly bulbous posterior end which encases the nascent end of the radular ribbon (q.v. previous section). The radular sac extends well behind the odontophore and is an extension of the radular sheath, formed from the subradular membrane. The buccal mass in *Persicula masirana* is morphologi-

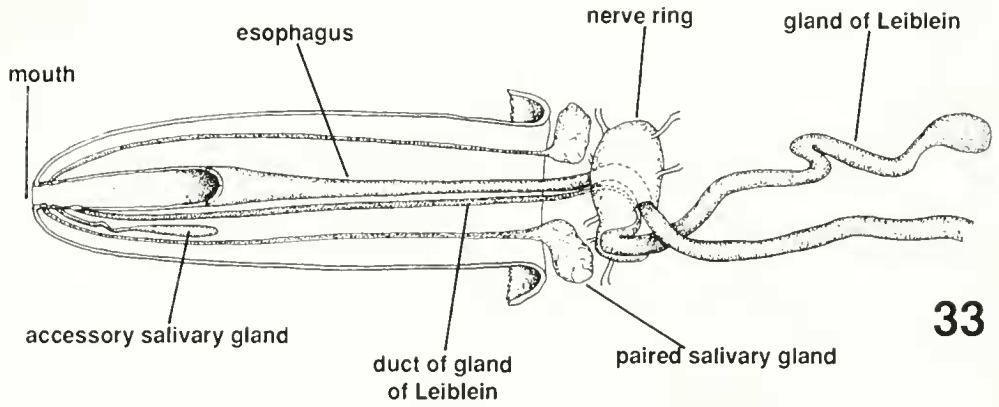


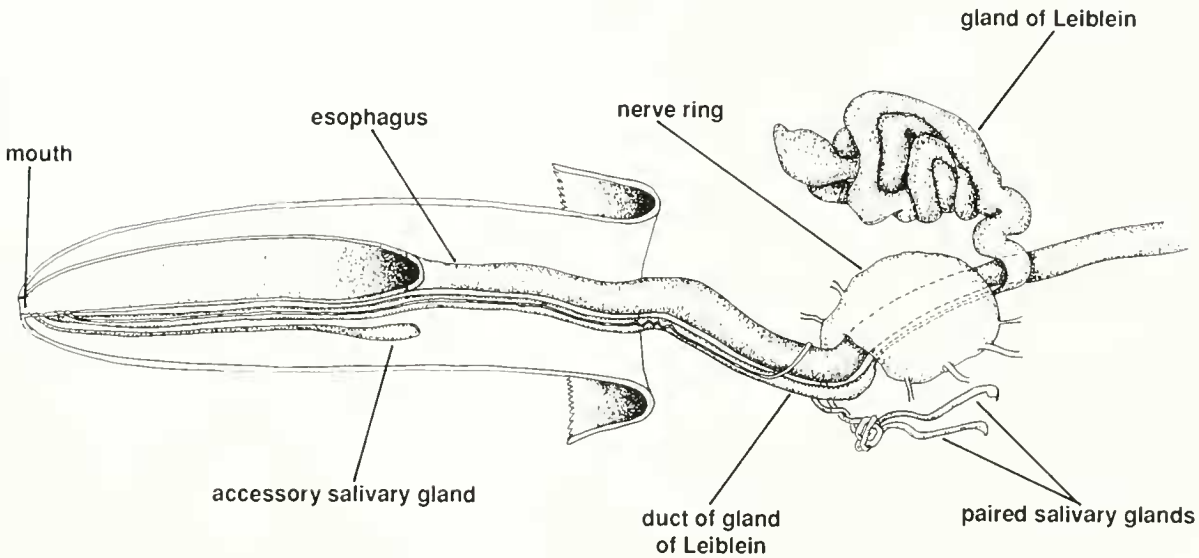


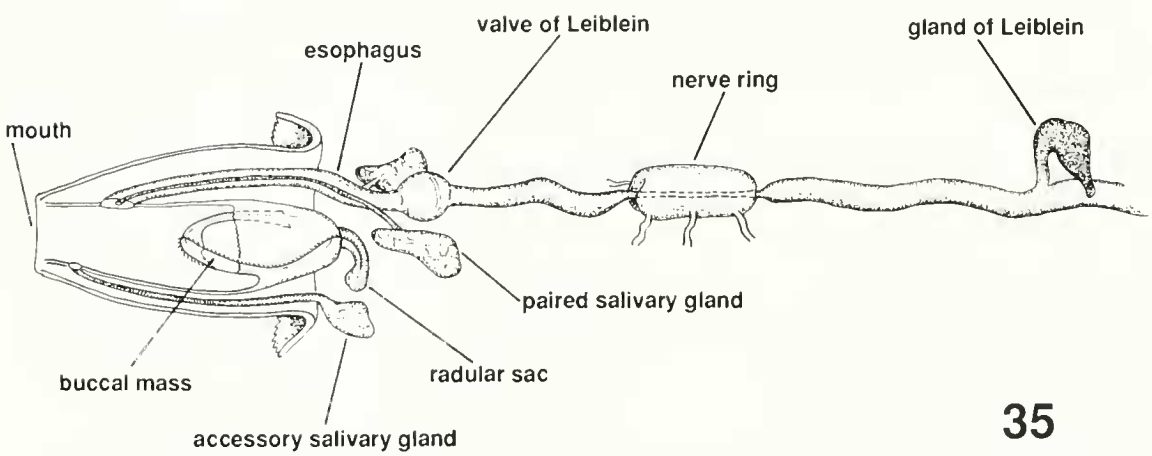
Figures 31–32. Anatomical features of the foregut of Prunini. Data in Table 1. **31.** *Prunum aff. aletes* Roth, 1978. 12.4 X. **32.** *Hyalina pallida* (Linné, 1758). 15.3 X.

cally the same, but the proboscis is simply longer, completely containing the radular sac. The characteristic shape and protrusion of the radular sac seems to be fairly typical for most Neogastropods (including Olividae), with the prominent exception being the Marginellidae, s. str. The radular sac thus differs in several respects from the buccal pouch of marginellids, especially in the lack of an anterior sphincter. All cystiscid genera studied have the same general type of radula, previously termed a cystiscid radula (q.v.). Based on the similar nascent ends of their radulae, all cystiscid genera are assumed to possess a true radular sac similar to that found in *Persicula* and *Gibberula*. A radular sac has actually been observed in several incompletely cleared cystiscid radulae, including the triserial group "*Cystiscus*," named as a new genus herein.

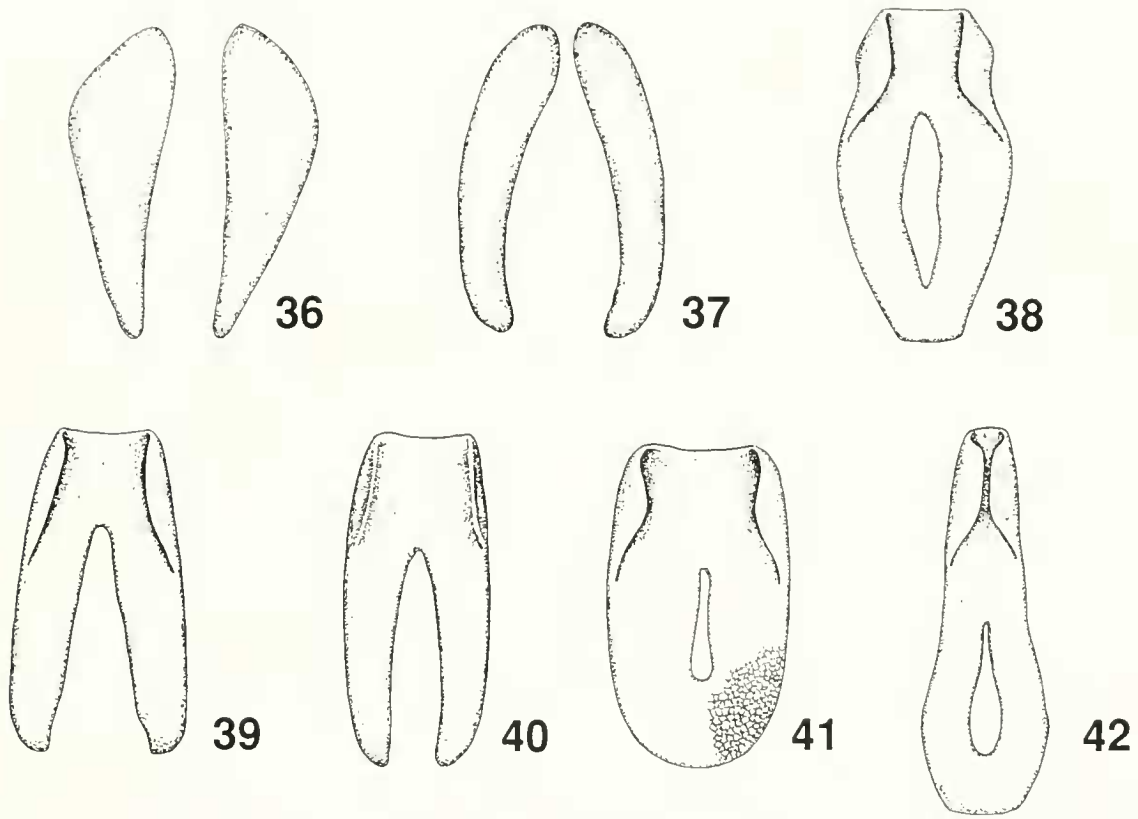
Odontophoral cartilages, which we prefer over "bolsters," "odontophore," or "cartilages," is a more specific term and clearly differentiates these structures from the odontophore, which is often used as a general term for the entire radular mass. These cartilages support and stiffen the radular mass and are composed of large Ley-







Figures 33–35. Anatomical features of the foregut of Marginellini and Persiculinae. Data in Table 1. **33.** *Dentimargo eburneola* (Conrad, 1834). 22.4 X. **34.** *Marginella glabella* (Linné, 1758). 5.2 X. **35.** *Persicula interruptolineata* (Megerle von Mühlfeld, 1816). 16.8 X.



Figures 36–42. Odontophoral cartilages of cystiscids and marginellids. Data in Table 1. **36.** *Persicula interruptolineata*. GAC 1581A. Length 0.97 mm. **37.** *Persicula masirana*. GAC Acc. # 4–94B. Length 1.01 mm. **38.** *Volvarina aff. avena*. GAC 1172B. Length 0.88 mm. **39.** *Prunum aff. aletes*. GAC 1518B. Length 1.50 mm. **40.** *Prunum guttatum*. GAC 1172A Length 0.75 mm. **41.** *Prunum prunum*. GAC 1582. Length 2.12 mm. **42.** *Prunum roosevelti*. GAC Acc. # 26–88A. Length 1.67 mm.

dig cells (chondroid tissue) by which they are easily recognized. Two fundamentally different conditions also exist in this character complex.

In all true marginellids examined, the two odontophoral cartilages are fused at least anteriorly, effectively functioning as a single structure underlying the radula. Ponder (1970:62) described the odontophoral cartilages in *Mesoginella pygmaea* as "fused into a single structure in the front half of the odontophore but posteriorly are connected by a transverse muscle in the usual way." Ponder (1970:66) described similarly fused cartilages in *Serrata aff. mustelina*, which are separated for only a short distance posteriorly. The two species of *Austroginella* discussed by Ponder and Taylor (1992:320) are likewise described as having anteriorly fused cartilages. The odontophoral cartilages in *Marginellona* were not described by Harasewych and Kantor (1991). Fretter (1976:329) simply described a single cartilage for *Volvarina taeniolata*. Our dissection of *V. aff. avena* revealed a pair of cartilages fused both anteriorly and posteriorly (figure 38). They are slightly bowed medially, leaving a medial slit about half the length of the entire structure, with the anterior margins raised and thickened, and truncated anteriorly. We suspect that *V. taeniolata* may be similarly structured. The closely related genus *Prunum* shows a similar condition. These structures were insufficiently described in Graham (1966) and Marcus and Marcus (1968) to draw any conclusions. Our dissections of four species of *Prunum* revealed that they all have strongly raised, thickened anterolateral margins, effectively forming a trough or channel for the radular ribbon (figure 20). The odontophoral cartilages in *P. roosevelti* (figure 42) are relatively narrow, rounded anteriorly, completely fused on the very long and narrow anterior half, and slightly bowed and narrowly fused posteriorly, confining a medial slit to the posterior half. The odontophoral cartilages in *Prunum prunum* (figure 41) are relatively short and broad, fused anteriorly and posteriorly, with a narrow medial slit. The anterior end is shallowly emarginate. *Prunum guttatum* (figure 40) and *P. aff. aletes* (figure 39) differ because their odontophoral cartilages are V-shaped, and narrowly fused anteriorly, but not posteriorly. The fused cartilages in *P. guttatum* (figure 40) have the posterior tips slightly convergent but not touching, with the anterior end truncate. In *P. aff. aletes* (figure 39), the anterior end is truncate to shallowly emarginate, and the posterior tips are divergent, forming a distinct V-shape, but in situ (figure 19) connective and muscle tissue hold these posterior tips closer together. In all cases, this fused pair of odontophoral cartilages underlies the main part of the radula (figures 19, 20). The radula wraps around the anterior

end of the odontophore, this point being effectively termed the bending plane. The shorter anterior portion of the radular ribbon, often showing broken cusps, thus lies under the anterior end of the odontophore, giving it the characteristic J-shape. Our data indicates that the odontophoral cartilage shape is consistent within each species, but differs between them, and may prove to be a useful taxonomic character.

All cystiscid genera examined have two completely separate odontophoral cartilages. Each cartilage fits into one of the lateral odontophoral cartilage hoods of the subradular membrane, flanking and not underlying the radula (figures 15, 16). Ponder (1970:70) described the odontophoral cartilages and muscle attachments for a species of *Gibberula*. Our dissections of *Persicula interruptolineata* (figure 36) revealed two separate subtriangular cartilages that are broad and rounded anteriorly, and narrowed posteriorly. In *P. masirana* (figure 37), the separate cartilages are elongate, rather uniform in width throughout, and pointed anteriorly. The radulae of nearly all other cystiscid genera have been described earlier in this paper, and most have odontophoral cartilage hoods. On this basis, we infer that they possess two separate odontophoral cartilages.

The anterior esophagus in radulate genera is situated dorsally within the proboscis, the buccal mass lying below it. In non-radulate species, the anterior esophagus is more centrally placed. Upon exiting the retracted proboscis posteriorly, the esophagus generally makes a sharp S-bend prior to passing through the nerve ring. A valve of Leiblein, when present, is located anterior to the circumesophageal nerve ring. Ponder and Taylor (1992:321) described the valve of Leiblein in *Austroginella* as being partially encased in the nerve ring anteriorly (figure 80). *Serrata* and *Mesoginella* have a well-developed valve located just anterior to the nerve ring. These three genera have a narrow, non-glandular bypass tube that is adherent ventrally to the valve of Leiblein. *Marginellona* has a large valve of Leiblein situated anterior to the nerve ring (figure 80). The two *Persicula* species we dissected also have a distinct valve of Leiblein, placed well anterior to the nerve ring (figure 35). No bypass tube was found. *Gibberula* has a similarly placed valve of Leiblein, but has a separate glandular tube that bypasses the valve (figure 79). *Volvarina*, *Hyalina*, *Prunum*, *Bullata*, *Dentimargo*, and *Marginella* all lack a valve of Leiblein. Marcus and Marcus (1968:65) discussed an "individually inconstant valve of Leiblein" in *Prunum martini*. In some *Prunum* species we dissected, what at first appeared to be a possible valve of Leiblein simply turned out to be food lumps in the esophagus that were inconsistent in their location or occurrence. We believe that the so-called "individually inconstant valve of Leiblein" in *Prunum martini* were simply food lumps in the esophagus of some individuals.

The esophagus narrows upon entering the nerve ring anteriorly, resuming its original size after exiting posteriorly. A much enlarged sac-like esophageal caecum was found just posterior to the nerve ring in all species of *Volvarina*, *Prunum* (figure 31), and *Bullata* studied. This structure was first described in *Prunum marginatum* as an "oesophageal caecum" (Graham, 1966:135, fig. 1). Eales (1923) did not mention this structure in *Hyalina hyalina*, nor was it mentioned by Coan and Roth (1976) for *H. pallida*. Our dissection of *H. pallida* (figure 32) revealed a thin-walled, but very distinct, esophageal caecum. An esophageal caecum is absent in all other marginelliform genera that have been studied anatomically.

The most conspicuous foregut gland is the gland of Leiblein, also called the "unpaired gland," "unpaired foregut gland," or "poison gland." This gland occurs in three different forms. In *Persicula* (figure 35) and *Gibberula* (figure 79), this gland is a small, short, often slightly folded gland emptying directly into the posterior end of the mid-esophagus, well posterior to the nerve ring. In *Marginellona* (figure 80), the gland of Leiblein is extremely large, sacculate, broad anteriorly and tapering posteriorly (Harasewych and Kantor, 1991:11). It also empties directly into the mid-esophagus posterior to the nerve ring. All the remaining marginelliform genera studied anatomically have a gland of Leiblein with a long, convoluted duct. The gland in these genera ends distally in a terminal bulb that is either rounded or weakly to distinctly pointed distally. The terminal bulb is narrow, elongate, and rounded distally in *Dentimargo* (figure 33). In *Marginella*, it is shorter, more swollen, and ends in an acuminate, pointed tip (figure 34). In *Serrata*, *Mesoginella*, and *Austroginella* (figure 80), the relatively large duct from the gland of Leiblein, which is about the same diameter as the esophagus, empties into the posterior end of the mid-esophagus just posterior to the nerve ring but does not pass through the nerve ring. These three genera also possess a well-developed valve of Leiblein with a ventral by-pass tube. In *Prunum* (figure 31), *Bullata*, *Volvarina*, *Hyalina* (figure 32), *Dentimargo* (figure 33), and *Marginella* (figure 34), the long, convoluted duct from the gland of Leiblein narrows as it passes through the nerve ring, then continues as a very narrow tube to the anterior end of the proboscis. These six genera all lack a valve of Leiblein. The duct from the gland of Leiblein empties either into the buccal cavity or into the extreme anterior end of the anterior esophagus, which is usually in very close proximity to the point where the ducts of the paired salivary glands empty into the buccal cavity. Ponder (1970:77, 79) described this duct in *Marginella desjardini* as opening "ventrally into the oesophagus a little in front of the nerve ring." This is in error because Graham (1966:139) clearly described this duct as opening "to the gut at almost the same level as that at which the salivary ducts reach the same position," which is at the "extreme anterior end of the proboscis, where they discharge, ... into the buccal cavity." This is mentioned because apparently a figure in Ponder (1973:fig. 3N) is based on this misconception. This does not weaken Ponder's hypothesis for the formation of the poison gland (Ponder, 1970:77–80), but it indicates that this intermediate stage is presently unknown.

All marginelliform genera have either tubular or ascinous paired salivary glands associated with the esophagus. In many cases, tubular and ascinous salivary glands appear to be found in different species of the same genus, and thus may be of limited taxonomic value in these genera. In all cases, the paired glands send fine, narrow ducts to the anterior end of the proboscis, where they empty into the buccal cavity. The placement of the glands and the attachment of ducts differ between species. In *Marginellona*, the paired salivary glands are found dorsal to the gland of Leiblein (figure 80), their ducts running anteriorly along the floor of the proboscis, free of the esophagus. *Serrata*, *Mesoginella*, and *Austroginella* all have glands that are attached to the esophagus just anterior to the valve of Leiblein, the ducts embedded in the esophageal walls for their entire length. *Volvarina taeniolata* has the glands free in the body cavity and the ducts free of the esophagus. In *V. aff. avena*, the paired salivary glands are relatively large and fully contained within the retracted proboscis, the ducts attached anteriorly to the esophagus. In *Prunum*, the paired salivary glands are free of the esophagus. In *P. prunum* and *P. guttatum*, the ducts are attached to the walls of the esophagus. In the other *Prunum* species studied, the ducts lay ventrally along the floor of the proboscis, free of the esophagus. Details on the salivary glands of *Bullata bullata* are unknown. The ducts in *H. pallida* are free of the esophagus, the glands apparently tubular but poorly preserved in the specimen studied. Both *Dentimargo* species have the glands largely contained within the proboscis. They are presumed to be tubular in *D. cairoma*, but are ascinous in *D. eburneola*. Oddly, these glands are not placed laterally in *D. eburneola* as is usual, but instead are placed dorsally and ventrally, one gland situated above the esophagus, the other below the accessory salivary gland (figure 33). In both species, the glands and their ducts lay free. The paired salivary glands of the three species of *Marginella* are located outside the proboscis near the nerve ring, free from the esophagus. In *M. glabella*, the ducts are attached to the duct of the gland of Leiblein (figure 34), unlike those of *M. sebastiani*. The paired salivary glands in *Persicula* and *Gibberula* are attached to the esophagus just anterior to the valve of Leiblein (figure 35). The ducts of *Persicula* are attached to the outside walls of the esophagus, but in *Gibberula* this is unknown. Ponder's illustration (1970: fig. 3E) seems to indicate that these ducts are embedded. Information on these glands and their ducts is summarized in Table 3.

The accessory salivary gland, when present, is always single and empties into the buccal cavity. It is present in all cystiscids studied, being ascinous in both species of *Persicula*, but tubular in *Gibberula*. Within marginellids, a tubular accessory salivary gland is present in *Serrata*, but absent in *Austroginella* and *Mesoginella*. A large, ascinous gland is present in *Volvarina aff. avena*, but appears to be tubular in *V. taeniolata* as described by Fretter (1976:329). Both species of *Hyalina* possess an accessory salivary gland, which is tubular in *H. hyalina* and apparently so in *H. pallida* (unreported in Coan & Roth, 1976 and poorly preserved in our specimen). An accessory salivary gland is present in only one species of *Prunum*, being tubular in *P. prunum*. The gland is present and tubular in *Dentimargo* and *Marginella*, but absent in *Marginellona*. Further work, including histology, is needed. See Table 3 for a summary of the occurrence of this gland.

Our primary objective was to discern useful taxonomic characters, and we feel that the most useful features are those of the foregut. Thus, the remainder of the digestive system was not studied in any greater detail by us, nor was the reproductive system. A brief summary of published information on these other systems follows.

The presence or absence of an anal gland should be further investigated. This structure was reported as present and extremely large in *Marginellona gigas* by Harasewych and Kantor (1991:11). *Serrata aff. mustelina*, *Mesoginella pygmaea*, *Dentimargo cairoma* (cf. Ponder, 1970), *Austroginella johnstoni*, *A. muscaria* (cf. Ponder & Taylor, 1992:322), and *Volvarina taeniolata* (cf. Fretter, 1976:329) were all reported as having an anal gland. The only marginelliform reported to lack an anal gland is the species of *Gibberula* reported by Ponder (1970: 71). Published accounts of the remaining species did not report the presence or absence of this structure.

Main features of the reproductive system were summarized in Harasewych and Kantor (1991:tables 2, 3). Published information on the reproductive system is incomplete for a number of species described anatomically. Probably of most interest in the female reproductive system is the presence of three glandular structures or seminal receptacles joining the pallial oviduct between the albumen gland and capsule gland in *Dentimargo cairoma* (cf. Ponder, 1970:74), whereas only one is present in *Gibberula* (op. cit., p. 75). Two such structures are the usual number, as recorded in *Mesoginella pygmaea* and *Serrata* aff. *mustelina* by Ponder (1970:74), *Marginellona gigas* by Harasewych and Kantor (1991:11), *Marginella desjardini* by Graham (1966:140), and *Volvarina taeniolata* by Fretter (1976:fig. 2A). Information is lacking for the other species. In the male reproductive system, the penis is normally simple, lacking appendages or lobes. But Ponder (1970:72, fig. 4C) described a bilobed penis for *Dentimargo cairoma* that has a sharply pointed posteroapical appendage, which he termed a sheath. Our dissection of *D. eburneola* likewise revealed a sharply pointed apical appendage, but the penis was not bilobed. The penis in *Bullata bullata* is an extremely large, simple, flattened, spatulate structure, about two-thirds the body length. All other species studied have a simple, unlobed penis. Refer to Harasewych and Kantor (1991:tables 2, 3) for a summary of additional characters.

Published information on marginelliform egg capsules was reviewed in Coovert (1986c and 1988e:42). Most marginelliform gastropods produce plano-convex or hemispherical egg capsules, but in *Persicula cornea* (Lamarck, 1822) and *Marginella goodalli* (G. B. Sowerby I, 1825) they are stalked. In most cases, each egg capsule

contains a single embryo, but *Prunum apicinum* (Menke, 1828) and *Dentimargo cairoma* sometimes have a second embryo, while egg capsules of *Volvarina avena* contain about five embryos. Development is direct in all known cases. All marginelliform species have a paucispiral protoconch indicating direct development.

Discussion: The division of marginelliform gastropods into two fundamentally different groups became obvious during the course of our research. These two groups were initially differentiated on gross radular features, but further research revealed differences in radular structure, anatomy, and internal columellar plications. In fact, these two groups can be differentiated on the basis of their internal shell whorls alone. These distinctly different groups are the cystiscids and the true marginellids. A brief summary of the differences follows.

Cystiscids have a shell that possesses what we have termed cystiscid internal whorls (figures 2, 3), or modified cystiscid internal whorls in *Granulina* (figure 4). These internal whorls are mostly resorbed by the animal, resulting in extremely thin, modified whorls. The anterior two or three columellar plications are reduced internally to a single, axially oriented, sharp edge. Within the aperture, the columella bears parietal lirae posterior to these plications, thus the columella is multiplicate. In *Granulina*, the posterior two columellar plications continue internally for a whorl or two and does not have a multiplicate columella. Cystiscid radulae (figures 13–16) are long, narrow, and C-shaped, with over 80 and up to 200 or more rachidian plates (with lateral teeth in one genus). The narrow rachidian plates have few cusps and are weakly to distinctly arched. The two odontophoral cartilages each fit into an anterolateral odontophoral cartilage hood (modified in *Granulina*), which flank the radula (figures 15, 16). The posterior end of the radula begins as a series of nascent rachidian plates. It is encased and secreted in a typical neogastropod radular sac, which extends beyond the end of the odontophore (figures 15, 35).

True marginellids, on the other hand, have unmodified internal whorls (figure 1). The plications are continuous internally and the columella is not multiplicate. Marginellid radulae (figures 17–20) are a much shorter, usually broad, uniserial, J-shaped ribbon with 10 to 80 rachidian plates. These moderately to very broad, flat to weakly arched plates usually have many cusps. The subradular membrane is weakly expanded anterolaterally into marginal cuticular flanges, which help hold the radula in correct alignment with the underlying, anteriorly fused odontophoral cartilages (figures 19, 20). The posterior end of the radula begins with only one or two preformed nascent rachidian plates which are secreted in the blind end of a buccal pouch. The odontophore extends past the posterior end of the radula (figure 19).

After discerning the two fundamentally different groups of marginelliform gastropods, we searched for possible relationships among other neogastropod families. This revealed that all of the above cystiscid characters are shared with the Olividae. Thus, we feel that the cystiscids have a shared ancestry with that family, and not with the Marginellidae (see final Discussion section for more details). We have come to the conclusion that the cystiscids and the true marginellids are not closely related and must be considered as separate and distinct families. A systematic section, outlining the classification of these two groups, follows.

SYSTEMATICS

Key to the Families of Marginelliform Gastropods

1a. Columellar plications not continuous internally, at least anterior two columellar plications reduced to one nearly axially oriented columellar edge within one full revolution internally; columella usually multiplicate with 3 (rarely 2) plications, plus often up to 14 parietal lirae posteriorly, but may have only 1 or 2 pseudocontinuous plications posterior to the anterior 2 internally reduced plications; internal whorls cystiscid or modified cystiscid type (figures 2, 3, 4) very thin and often partially missing due to partial resorption ..... family CYSTISCIDAE

1b. Columellar plications continuous internally, not reduced; columella with 2 to 6 plications, at least the first 4 continuing internally, the 5th and 6th often not continuing internally (and are thus parietal lirae); internal whorls unmodified type (figure 1) complete and of original thickness, without evidence of resorption .... family MARGINELLIDAE

Family CYSTISCIDAE Stimpson, 1865:55

Diagnosis: Shell minute to large, white, uniformly colored, or patterned; surface smooth, sculptured, or axially costate; spire flat to immersed, or low to tall; protoconch paucispiral; lip thickened, smooth or denticulate; external varix present or absent; siphonal notch present or absent; posterior notch present or absent; columella multiplicate, with combined total of 2 to 13 plications + parietal lirae or with 2 internally reduced columellar plications + 1 or 2 pseudo-continuous plications; internal whorls cystiscid or modified cystiscid type. Type 2, 3, or 4 animal; operculum absent. Cystiscid radula, Type 1, 2, 3, or 4. Mantle cavity with monopectinate ctenidium and bipectinate osphradium. Proboscis pleurembolic; jaws absent; typical radular sac present.

Remarks: The family was erected by Stimpson (1865: 55) for a single included species based on unusual features of the head and radula. Subsequent authors included this group in the Marginellidae. Coan (1965:186) recognized this group as a subfamily, again based on unusual features of the head and radula, but did not include such genera as *Gibberula* (in part), *Persicula*, and *Canalispira*. Rules of priority require this name to be used, which is unfortunate because the type specimen of the type species

is lost (Coovert, 1986d) and the species is otherwise poorly known. We currently recognize 283 species in the Cystiscidae, of which 26 are undescribed.

Key to the Recent Genera of the Family Cystiscidae

1a. Distinct siphonal notch present; spire low to immersed; shell minute to small 2
1b. Siphonal notch absent, anterior end rounded; spire immersed, low, or distinctly produced; shell minute to large 3
2a. Adult shell completely lacking an external varix; spire low to nearly immersed, but never completely immersed; shell usually white, uniformly colored in some, rarely with a few narrow spiral bands ..... *Gibberula*
2b. Adult shell completely lacking an external varix or with an obscure to distinct, raised external varix; spire usually completely immersed, rarely very low; shell usually uniformly colored or with distinctive pattern of spots, tear-drop markings, longitudinal or oblique streaks or zig-zag lines; narrow spiral bands, if present, very numerous; rarely white, if so, with pattern ..... *Persicula*
3a. External varix completely absent; columella multiplicate, with combined total of 2 to 17 plications + parietal lirae; with cystiscid internal whorls ... 4
3b. External varix present, distinct, raised, usually strong; columella with 2 internally reduced anterior plications + 1 or 2 pseudo-continuous plications; with modified cystiscid internal whorls ... 8
4a. Posterior corner of aperture sharply, narrowly, and deeply channeled; aperture usually lirate, smooth in some; sutures often channeled or impressed, if filled with callus, then still distinct; spire distinctly produced ..... *Canalispira*
4b. Posterior corner of aperture rounded, not channeled; aperture smooth or denticulate, not lirate; sutures callused over, indistinct; spire immersed or low 5
5a. Shell with very strong, sharply crested axial costae; strongly developed parietal callus "shield" present; spire sunken, but not immersed, with nuclear whorls visible; 5 columellar plications present; lip heavily thickened, flared posteriorly, not denticulate ..... *Extra*
5b. Shell lacking strong axial costae, although may have very weak axial growth lines or very faint wrinkles; parietal callus wash often present, but lacking strongly developed parietal "shield"; spire produced or completely immersed, but not as above; combined total of 2 to 17 columellar plications + parietal lirae; lip narrowly to strongly thickened, smooth or weakly denticulate 6
6a. Suture of last whorl expanding rapidly for final half whorl, then abruptly swept posteriorly just before lip, giving characteristic shape to shell; spire nearly flat to low, not immersed; shell shape usually cylindrical, elliptic, or oblong ..... *Plesiocystiscus*
6b. Suture of last whorl not unusually expanding or narrowing; spire low to completely immersed; shell shape rarely cylindrical, usually elliptic, obovate to broadly obovate, or subtriangular 7
7a. Spire usually immersed; plications usually square in cross-section, often appearing excavated due to collabral parietal callus ridge, which intersects them just outside of aperture ..... *Crithe*
7b. Spire usually at least slightly produced; plications usually rounded in cross-section, rarely appearing excavated, if so, not due to collabral parietal callus ridge ..... *Cystiscus*
8a. Shell usually smooth, if sculptured, very obscure; spire immersed; shell elongate to broadly elliptic, obovate, subtriangular, or pyriform, not cylindrical ..... *Granulina*
8b. Shell with distinct, punctate sculpture; spire flat to immersed; shell broadly cylindrical and abruptly narrowed anteriorly to broadly subtriangular ..... *Pugnus*

Subfamily PLESIOCYSTISCINAE Coovert and Coovert, new subfamily

Diagnosis: Shell minute to small, white, hyaline; last whorl rapidly expanded then lip abruptly swept posteriorly giving characteristic shape; spire flat to low; lip thickened posteriorly, smooth, lacking lirae or denticulation; external varix absent; siphonal notch absent; posterior notch absent; columella multiplicate with combined total of 3 to 8 plications + parietal lirae; internal whorls cystiscid type. Type 2 animal; tentacles and siphon moderately long; mantle translucent, in some species not readily extending over external shell surface; foot relatively narrow. Type 1 radula. Internal anatomy unknown.

Genus *Plesiocystiscus* Coovert and Coovert, new genus (figures 3, 21, 43)

Type species: *Marginella jewettii* Carpenter, 1857a; OD, herein (figure 43).

Diagnosis: Same as for subfamily.

Description: Shell (figures 3, 43) minute to small, (adult length 1.5–6.0 mm). Color white, hyaline; surface smooth, glossy. Shape cylindrical, elliptic, or obovate; weakly to distinctly shouldered. Suture rapidly descending on last half of last whorl, then abruptly sweeping upward just before lip, giving characteristic shape to adult shell. Spire nearly flat to low. Aperture moderately narrow, broader anteriorly. Lip thin anteriorly, gradually thickening toward shoulder, smooth, lacking denticulation or lirae, external varix absent. Siphonal notch and posterior notch absent. Shell often with a weak parietal callus wash or weak parietal callus deposits. Columella multiplicate, with combined total of 3–8 plications + parietal lirae, usually

occupying less than half to slightly more than half the aperture length. Shell with cystiscid internal whorls.

External anatomy: 4 species studied. Type 2 animal, with moderately long tentacles; eyes at base of tentacles; siphon simple, moderately long; mantle translucent and barely visible, possibly not extending over external shell surface in some species; foot relatively narrow, about as wide as shell and 1½ times shell length; animal variously marked with tiny dots of various colors, pattern of internal mantle showing through translucent shell.

Internal anatomy: Unknown.

Radula (figure 21): 3 species studied. Type 1, triserial, with simple, thin, weak laterals that narrow to a single cusp. Ribbon long, narrow, composed of 66–103 rows of plates. Rachidian plates overlapping, very narrow (0.017–0.028 mm wide), weakly arched, with 3–7 sharp cusps on posterior edge. Anterior edge of rachidian plate slightly concave, resulting in weakly U-shaped plates. Shell length: radular width ratio (based on rachidian plate width) = 159–200. Radular Index = 10.9–34.3.

Included species: *P. abbotti* (Jong & Coomans, 1988), *P. atomus* (E. A. Smith, 1890), *P. bubistae* (Fernandes, 1987), *P. cinereus* (Jousseaume, 1875), *P. consanguineus* (E. A. Smith, 1890), *P. gutta* (Gofas & Fernandes, 1988), *P. jansseni* (Jong & Coomans, 1988), *P. jewettii* (Carpenter, 1857), *P. josephinae* (Fernandes & Rolan, 1992), *P. larva* (Bavay, 1922), *P. palantirulus* (Roth & Coan, 1968), *P. politulus* (Dall, 1919), plus 4 undescribed species.

Distribution and Habitat: Indo-Pacific (1 species), E. Pacific (4 species), western Atlantic (5 species), W. African (6 species). Intertidal to 80 m.

Fossil Record: Eocene of France, Miocene and Pliocene of Florida, and Pleistocene of California, to Recent.

Nomenclature, Synonymy: Photographs of the syntypes of the type species, *Marginella jewettii*, were published by Palmer (1958:pl. 24, figs. 19–21). A lectotype was designated and illustrated in Coan and Roth (1966:pl. 51, fig. 66). The genus name is derived from the Greek *plesios*, near, in the sense of plesiomorphic, of characters near the ancestor, combined with *Cystiscus*. This indicates the relationship to (and previous inclusion in) the genus *Cystiscus*, type genus of the family. The triserial radula, found in many other neogastropod families, but unknown in any other cystiscids, is the most primitive in this family. Gender masculine.

Remarks: This is the only genus of marginelliform gastropods (previously referred to as "*Cystiscus*") with a triserial radula. This group is considered to be the most primitive in the family based on the radula and possession of a generalized Type 2 animal. Radular and shell features, including presence of odontophoral cartilage hoods, possession of cystiscid internal whorls, and lack of an external varix, place this group in the Cystiscidae.

Gofas and Fernandes (1988:19) described the mantle of *P. gutta* (Gofas & Fernandes, 1988) as "translucent and hardly visible when it extends over the shell." Roth and Coan (1968:66) observed that "the mantle was never extruded over the top of the shell of *C. jewettii*" and Behrens (1984:241) likewise described the mantle as not covering the shell in the same species. Additional observations on this point would be useful.

Subfamily CYSTISCINAE Stimpson, 1865:55

Diagnosis: Shell minute to small, white; spire immersed to low; surface smooth or axially costate; lip thickened, smooth or denticulate; external varix absent; siphonal notch absent; posterior notch absent; columella multiplicate, with combined total of usually 2 to 8 plications + parietal lirae; internal whorls cystiscid type. Type 3 animal; mantle smooth, at least partially extending over external shell surface. Type 2 radula. Internal anatomy unknown.

† Genus *Topaginella* Laseron, 1957

Topaginella Laseron, 1957:288

Type species: *Marginella octoplicata* Tenison-Woods, 1877 †; OD (M)

Diagnosis: Shell minute, pyriform, strongly narrowed anteriorly; spire low; lip thickened, strongly denticulate; external varix absent (?); distinct axial costae present; siphonal notch absent; columella multiplicate, with combined total of usually 8 plications + parietal lirae.

Fossil Record: Miocene of Australia.

Nomenclature, Synonymy: The type species, *T. octoplicata*, was figured in Cotton (1949:pl. 18).

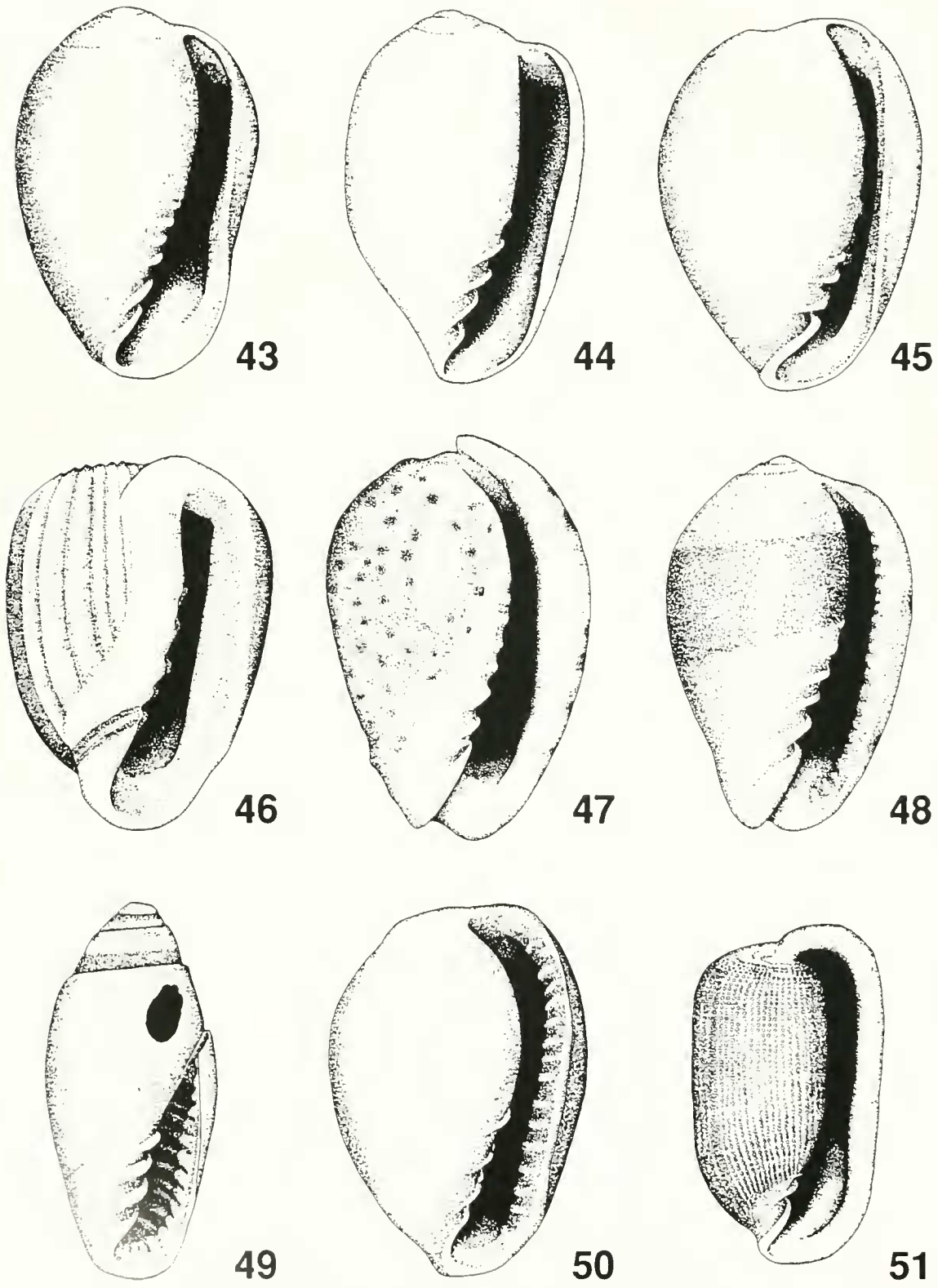
Remarks: The type species seems to be unique. The multiplicate columella and lack of a siphonal notch place it near *Cystiscus*, but the pyriform shape, exserted spire, denticulate lip, and fine axial costae ("striated growth lines" of Cotton, 1949:218) render it distinct. The absence of an external varix needs to be confirmed.

Genus *Cystiscus* Stimpson, 1865
(figures 9, 10, 22, 44)

Cystiscus Stimpson, 1865:55
Euliginella Laseron, 1957:282 [TS: *Marginella angasi* Crosse, 1870; OD]

Type species: *C. capensis* Stimpson, 1865 (non *Marginella capensis* Krauss, 1848), = *Marginella cystiscus* Redfield, 1870 (nom. nov.); M (figure 44).

Diagnosis: Shell minute to small, white, hyaline; spire immersed to low; lip thickened, smooth or weakly denticulate; external varix absent; siphonal notch absent; posterior notch absent; lacking collabral parietal callus ridge; columella multiplicate, with combined total of



Figures 43–51. Shells of type species of cystiscid genera, ventral views. **43.** *Plesiocystiscus jewettii* (Carpenter, 1857). GAC M1823, Pirates Cove, San Luis Obispo, California, intertidal. Length 5.3 mm. **44.** *Cystiscus cystiscus* (Redfield, 1870). Holotype (destroyed), False Bay, Cape of Good Hope, South Africa, 37 m, on gorgonians. After Stimpson (1865:pl. 8, fig. 2). Length 3.6 mm. **45.** *Crithe atomaria* Gould, 1860. ANSP 307869, 1.6 km W.S.W. of Pulau Blankang Matti, Singapore, Malaya. Length 2.0 mm. **46.** *Extra extra* Jousseaume, 1894. P. W. Clover colln., Perim, South Yemen. Length 0.9 mm. **47.** *Persicula persicula* (Linné, 1758). GAC

usually 2 to 8 plications + parietal lirae, 1st plication usually strong and raised. Type 3 animal; mantle smooth, at least partially extending over external shell surface.

Description: Shell (figure 44) minute to small (adult length 1.0–6.0 mm). Color white, hyaline; surface smooth, glossy. Shape rarely cylindrical, usually elliptic, obovate, or subtriangular; weakly shouldered. Spire completely immersed to low. Aperture narrow to broad, usually wider anteriorly. Lip slightly to distinctly thickened, flared posteriorly in some species, smooth on inside edge to weakly denticulate, lacking lirae, external varix absent. Shell lacking a siphonal notch and posterior notch. Shell with weak parietal callus wash or weak parietal callus deposits in some species, but lacking collabral parietal callus ridge. Columella multiplicate, with combined total of 2–8 plications + parietal lirae, rarely up to 17 in which the posteriormost are denticles; one species with only 1 plication. Plications usually occupying less than half the length of the aperture, but most of the aperture in some. Plications excavated just inside aperture in a few species, usually evenly rounded, first plication usually raised and very strong. Shell with cystiscid internal whorls.

External anatomy (figures, 9, 10): 13 species studied. Type 3 animal with eyes at side of head, usually on lateral swelling; mantle smooth, at least partially extending onto external shell surface, in some species nearly covering shell; foot relatively narrow, about as wide as shell and 1–1.5 X shell length; head and mantle usually uniformly colored, often bright red, orange, or yellow, or brown or black, internal mantle color pattern often showing through translucent shell.

Internal anatomy: Unknown.

Radula (figure 22): 14 species studied. Type 2, uniserial, ribbon long, narrow, composed of 80–200 plates. Rachidian plates overlapping (rarely separate), very narrow (0.009–0.036 mm wide), weakly to strongly arched, with 5–15 very strong cusps on posterior edge. Anterior edge of rachidian plate slightly concave, resulting in crescent-shaped plates. Shell length: radular width ratio = 94–217. Radular Index = 10.7–25.7.

Distribution and Habitat: Neozelanic (1 species), So. Australian (21 species), Indo-Pacific (11 species), W. Atlantic (2 species), South African (23 species). Intertidal to 370 m.

Fossil Record: Eocene of France, Miocene and Pliocene of Australia, to Recent.

Nomenclature, Synonymy: The type species *C. cystiscus* is discussed and figured in Coovert (1986d) and herein (figure 44). The radula of this species, along with three others, was reviewed in Coovert (1989b:5–6). SEMs of an additional eight Australian species (Dean Hewish, pers. comm.), including *C. angasi*, the type species of *Euliginella*, have been examined by us. All these species are considered congeneric based on similar radulae and shell characters. *Euliginella* was considered synonymous by Coan (1965:190).

Remarks: Originally described in its own family by Stimpson, apparently based on the radula and unusual features of the head, this genus again becomes the nominate genus of a now more clearly defined family.

Genus *Crithe* Gould, 1860
(figure 45)

Crithe Gould, 1860:384
Microvulina Habe, 1951:105 [TS: *M. nipponica* Habe, 1951; OD]

Type species: *C. atomaria* Gould, 1860; M (figure 45)

Diagnosis: Shell minute to small, white, hyaline; spire usually immersed, rarely low; lip thickened, smooth, lacking denticulation; external varix absent; siphonal notch absent; posterior notch absent; columella multiplicate, with combined total of 6–8 plications + parietal lirae, plications usually excavated inside aperture due to collabral parietal callus ridge. Presumably a Type 3 animal.

Description: Shell (figure 45) minute to small (adult length 1.6–3.2 mm). Color white, hyaline; surface smooth, glossy. Shape narrowly to broadly obovate or subtriangular; weakly to moderately strongly shouldered. Spire usually completely immersed, rarely low. Aperture narrow, wider anteriorly. Lip moderately thickened, especially posteriorly, thinner anteriorly, smooth on inside edge, lacking denticulation and lirae, external varix absent. Shell lacking a siphonal notch and posterior notch. Shell usually with a distinct collabral parietal callus ridge that intersects plications. Columella multiplicate, with combined total of 6–8 plications + parietal lirae, usually occupying about two-thirds the aperture length. Plications usually appearing excavated just inside aperture due to callus deposits from anterior end of collabral parietal callus ridge. Shell with cystiscid internal whorls.

External anatomy: Presumably a Type 3 animal; mantle extension undetermined; generally uniformly colored, bright yellow, rose, or orange-red, or black with 2 zones of yellow on internal mantle.

←

M1558, Dakar, Senegal, West Africa, in sand, low tide. Length 20.0 mm. **48.** *Gibberula oryza* (Lamarck, 1822). Neotype, MHNG, Senegal. After Gofas (1990:fig. 2). Length 6.5 mm. **49.** *Canalispira olivellaeformis* Jousseaume, 1875 Lectotype, MHNP, locality unknown. After photos in Kilburn (1990:fig. 5). Length 4.2 mm. **50.** *Granulina isseli* (G. & H. Nevill, 1875). GAC Acc. # 53–87, Red Sea coast of Egypt between El Ghurdaga and 80 km south of El Quseir. Length 1.6 mm. **51.** *Pugnus parvus* Hedley, 1896. GAC M2135, east of North Pt., Flinders Island, Bass Strait, Australia, 39°43'S, 148°36'E. Length 2.0 mm.

Internal anatomy: Unknown.

Radula: 1 species studied (3 specimens). Type 2, uniserial, ribbon long, narrow, composed of 189–220 plates. Rachidian plates overlapping, very narrow (0.007–0.008 mm wide), weakly arched, with 4 strong cusps on posterior edge. Anterior edge of rachidian plate slightly concave, resulting in an asymmetrically V-shaped plate. Shell length: radular width ratio = 234–270. Radular Index = 47.2–55.0.

Distribution and Habitat: Indo-Pacific (6 species). Intertidal to 58 m.

Fossil Record: Pliocene of Australia to Recent.

Nomenclature, Synonymy: The type species of *Crithe* and *Microvulina*, and their generic synonymy, were discussed in Coovert (1986e and 1987c). The holotype of *C. atomaria* was figured in Johnson (1964:pl. 8, fig. 12) and Coovert (1986e:fig. 1).

Remarks: The columellar plications, which are square in cross-section and excavated due to the collabral parietal callus ridge, and the usually immersed spire, serve to differentiate this group. The radulae are diagnostic.

Genus *Extra* Jousseaume, 1894
(figure 46)

Extra Jousseaume, 1894:98, 101

Type species: *E. extra* Jousseaume, 1894; M (figure 46)

Diagnosis: Shell minute, white, semitranslucent; prominent axial costae present; spire sunken but not immersed; lip strongly thickened, smooth, lacking denticulation, flared posteriorly; siphonal notch absent; posterior notch absent; distinct parietal callus "shield" present; columella multiplicate, with combined total of 5 plications + parietal lirae, plications slightly excavated inside aperture due to parietal callus deposits.

Description: Shell (figure 46) minute (adult length 1.3–1.4 mm). Color white, body whorl semitranslucent, surface with 17–20 prominent, sharply crested axial costae. Shape obovate, truncate posteriorly; strongly shouldered. Spire sunken but not immersed. Aperture narrow, slightly wider anteriorly. Lip very strongly thickened, especially posteriorly, arched above apex and flared posteriorly, smooth on inside edge, lacking denticulation and lirae, apparently lacking an external varix. Shell lacking a siphonal notch and posterior notch. Shell with a distinct parietal callus "shield" that is free anteriorly with slight chink behind. Columella multiplicate, with combined total of 5 plications + parietal lirae occupying about ¾ the aperture length. Plications slightly excavated just inside aperture due to callus deposits from the parietal callus shield. Internal whorls unknown but presumed to be cystiscid type.

External anatomy: Unknown.

Internal anatomy: Unknown.

Radula: Unknown.

Distribution and Habitat: Indo-Pacific (1 species), recorded only from the western Indian Ocean. Apparently shallow water.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: See Coovert (1987d) for discussion.

Remarks: This monotypic genus is provisionally placed in the Cystiscinae based on the 5 excavated plications and lack of labial denticulation. The last strong axial costa has the appearance of an external varix, which, if present, might eliminate this genus from the Cystiscinae. The slightly sunken but non-immersed spire and the parietal "shield" of this group appear to be unique.

Subfamily PERSICULINAE Coovert and Coovert, new subfamily

Diagnosis: Shell minute to large, white, uniformly colored, or patterned; spire immersed or low to tall; lip thickened, smooth or lirate; external varix present or absent; siphonal notch present or absent; weak to distinct posterior notch present; columella multiplicate with combined total of 3–13 plications + parietal lirae; internal whorls cystiscid type. Type 4 animal; tentacles short to long, rarely absent; siphon short to long; eyes situated laterally on head slightly below the base of the tentacles; mantle usually not extending over external shell surface. Type 3 radula. Odontophoral cartilages separate; valve of Leiblein present, with or without bypass tube; esophageal caecum absent; gland of Leiblein short, small, emptying directly into posterior end of esophagus; paired salivary glands ascinous or tubular, attached to esophagus just anterior to the valve of Leiblein, ducts attached to walls of esophagus; single accessory salivary gland present, ascinous or tubular; anal gland absent.

Genus *Persicula* Schumacher, 1817
(figures 2, 11–16, 23, 35–37, 47)

Persicula Schumacher, 1817:235
Pachybathron Gaskoin, 1853:356 [TS: *P. marginelloideum* Gaskoin, 1853, = *Erato cypracoides* C. B. Adams, 1845, SD (M) Tryon, 1885:270]
Persicula, subg. *Rabicea* Gray, 1857:37 [TS: *P. interrupta* (Lamarck, 1822), = *Marginella interrupta* Lamarck, 1822, = *Voluta interruptolineata* Megerle von Mühlfeld, 1816; M]

Type species: *P. variabilis* Schumacher, 1817, = *Voluta persicula* Linné, 1758; M (figure 47)

Diagnosis: Shell small to large, uniformly colored, or white to colored and patterned, moderately thick to thick-shelled; spire usually immersed; lip thickened, weakly to strongly lirate; external varix present or absent; distinct siphonal notch present; posterior notch present; columella multiplicate with combined total of 4–13 plications

+ parietal lirae. Type 4 animal; tentacles long; siphon usually long; mantle apparently not extending over external shell surface.

Description: Shell (figures 2, 47) small to large (adult length 4.5–34.0 mm). Color white, tan, pinkish- or yellowish-tan, to gray, with pattern of spiral lines, rows of dots or tear-drop shaped markings, or longitudinal wavy or zig-zag markings which often form triangular peaks, less often uniformly flesh-colored or nearly white due to pattern reduction; surface smooth, glossy, few species with weak axial costae. Shape narrowly to broadly obovate, or narrowly to broadly elliptic; weakly to moderately strongly shouldered. Spire usually completely immersed, rarely slightly produced. Aperture narrow, slightly wider anteriorly. Lip moderately thickened, especially posteriorly, thinner anteriorly, very weakly to strongly lirate, completely lacking an external varix or with strong to weak external varix. Shell with a distinct siphonal notch and a very weak to very distinct posterior notch. Moderately-thick to thick-shelled, some species with distinct parietal or apical callus deposits, a few with a very strong parietal callus "shield." Columella multiplicate, with combined total of 4–13 plications + parietal lirae usually occupying more than half the aperture length. Shell with cystiscid internal whorls.

External anatomy (figures 11, 12): 15 species studied. Type 4 animal with moderately long to long tentacles, siphon simple, moderately short to usually very long; mantle apparently not extending over external shell surface; foot narrow to moderately broad, about as wide as shell to considerably broader and about 1½ times shell length; animal variously marked with tiny dots, spots, blotches, flecks, or streaks of opaque white, black, or various colors.

Internal anatomy (figures 35–37): 2 species studied. As in family diagnosis. Valve of Leiblein without bypass tube, paired salivary glands ascinous, single accessory salivary gland ascinous.

Radula (figures 13–16, 23): 14 species studied. Type 3, uniserial, ribbon long, narrow, composed of 80–209 plates. Rachidian plates overlapping, narrow (0.011–0.093 mm wide), moderately to strongly arched, with 6–14 sharp cusps on posterior edge, the central cusp usually the strongest. Anterior edge of rachidian plate strongly concave, resulting in U- or V-shaped plates. Shell length: radular width ratio = 146–572. Radular Index = 6.7–21.8.

Distribution and Habitat: S. Australian (3 species), Indo-Pacific (11 species), E. Pacific (7 species), W. Atlantic (20 species), W. African (9 species), South African (1 species).

Fossil Record: Eocene of France and Alabama, upper Oligocene and Miocene of W. Atlantic, to Recent. Intertidal to 370 m.

Nomenclature, Synonymy: The type species of *Rabicea*, *V. interruptolineata*, is congeneric with *P. persicula*, based on similar shell, radular (Coovert, 1989b:22), and external anatomical features. Coan and Roth (1966:282) discussed this synonymy. *Pachybathron* has been treated as a valid genus by many recent authors, including Coomans (1972), who discussed the group, its early confused familial placement, the type species, and its synonymy. The cited example in Adams and Adams (1853:194) does not constitute a type fixation. Tryon (1885:270) thus provided the earliest type fixation by subsequent designation. The features of the external anatomy, radula, and the brown triangular markings of the shell indicate a close relationship to some of the other small western Atlantic *Persicula*. The parietal callus shield is considered to be no more than a species-group character. Thus, *Pachybathron* is here treated as a synonym. Subgeneric recognition may eventually be justified, but this would necessitate formal recognition of other species groups, a step considered unwise at this time.

Remarks: Erroneously reported to have a Type 2 animal (Coovert, 1987g, 1987i) based on strictly dorsal views, closer examination of several species revealed the split head typical of a Type 4 animal (figure 11). The two halves of the head are capable of closing together at will, thus appearing unsplit. The long siphon usually distinguishes this group anatomically from the closely related *Gibberula*. The shell of *Persicula* is usually patterned, often has a distinct external varix, and the spire is usually immersed. These conchological features serve to separate the two groups and are presented in the key to Recent genera. See Coovert (1987b) for a discussion of the *Persicula cornea* group.

Genus *Gibberula* Swainson, 1840
(figures 48, 79)

Gibberula Swainson, 1840:323
Granula Jousseaume, 1875:167, 246 [TS: *G. bensoni* (Reeve, 1865), = *Marginella bensoni* Reeve, 1865; SD (M) Coan, 1965: 190]
Kogomea Habe, 1951:103 [TS: *Marginella novemprovincialis* (Yokoyama, 1928), = *Erato novemprovincialis* Yokoyama, 1928; OD]
† *Dentiginella* Laseron, 1957:288 [TS: *Marginella metula* Cotton, 1949 †; OD (M)]
Epiginella Laseron, 1957:279 [TS: *E. ablata* Laseron, 1957; OD]
† *Lataginella* Laseron, 1957:288 [TS: *Marginella kitsoni* Chapman, 1921 †; OD (M)]
Phyloginella Laseron, 1957:280 [TS: *P. compressa* Laseron, 1957; OD]
† *Vetaginella* Laseron, 1957:288 [TS: *Marginella doma* Cotton, 1949 †; OD (M)]
Diluculum Barnard, 1962:14 [TS: *D. inopinatum* Barnard, 1962, = *Marginella bensoni* Reeve, 1865; OD]

Type species: *G. zonata* Swainson, 1840, = *Volvaria oryza* Lamarck, 1822; M (figure 48)

Diagnosis: Shell minute to medium size, white or colored, some species with spiral bands; spire low to medium height, not immersed; lip thickened, weakly to strongly

lirate, smooth in some species; external varix absent; distinct siphonal notch present; posterior notch present but often weak; columella multiplicate with combined total of 3–8 plications + parietal lirae. Type 4 animal; tentacles short; siphon short; mantle not usually extending over external shell surface.

Description: Shell (figure 48) minute to medium in size (adult length 1.8–8.5 mm). Color usually white, hyaline, less commonly tan, yellow, or orange, some species with spiral lines or bands or sutural band, rarely with oblique markings; surface smooth, glossy, rarely with fine, weak axial costae. Shape narrowly subcylindrical to usually elliptic, obovate, or subpyriform; weakly to strongly shouldered, some species with weakly raised sutures. Spire low to medium height, not immersed. Aperture narrow to moderately broad, wider anteriorly. Lip moderately thickened, especially posteriorly, thinner anteriorly, usually weakly to strongly lirate but absent in some species, completely lacking an external varix. Shell with distinct siphonal notch and very weak to distinct posterior notch. Shell with apical callus deposits in some species, rarely with elongate collabral parietal callus deposits. Columella multiplicate, with combined total of 3–8 plications + parietal lirae occupying ⅓ to nearly the full aperture length. Shell with cystiscid internal whorls.

External anatomy: 26+ species studied. Type 4 animal, with short tentacles, which are rarely absent; siphon simple, short, barely extending above the dorsal edge of the siphonal notch; mantle apparently not extending over external shell surface or with a small lobe on the left side in some species; foot narrow to moderately broad, about as wide to slightly wider than shell and usually about 1½ times shell length; some species with anterolateral edges of foot weakly to strongly raised to form "parapodia"; animal variously marked with tiny dots, spots, or blotches, but not striped or lineated, markings of opaque white, brown, yellow, orange, or green.

Internal anatomy (figure 79): 1 species studied. As in family diagnosis. Valve of Leiblein with bypass tube; paired salivary glands tubular; single accessory salivary gland tubular.

Radula: 21 species studied. Type 3, uniserial, ribbon long, narrow, of 80–153 plates. Rachidian plates overlapping, narrow (0.008–0.042 mm wide), moderately to strongly arched, with 5–11 sharp cusps on posterior edge. The central cusp is usually the strongest. Anterior edge of rachidian plate strongly concave, resulting in U- or V-shaped plates. Shell length: radular width ratio = 118–309. Radular Index = 9.1–21.9.

Distribution and Habitat: Neozelanic (2 species), S. Australian (4 species), Indo-Pacific (26 species), E. Pacific (6 species), W. Atlantic (9 species), Mediterranean (10 species), W. African (25 species), South African (7 species). Intertidal to 3,300 m.

Fossil Record: Paleocene and Eocene of France and W. Atlantic, Miocene and Pliocene of Italy, Australia, W. Atlantic, and Japan, and Pleistocene of W. Atlantic and California, to Recent.

Nomenclature, Synonymy: *Gibberula oryza*, type species of this genus, is valid and distinct from *G. miliaria* (Linné, 1758). Coan (1965:189) (questionably) and Dodge (1955:79–82) considered these two species synonymous. But Gofas (1990:117) clearly differentiated the two species based on shell and external anatomical characters, and designated a neotype (figure 48) and lectotype respectively. The genus *Granula* and its type species *M. bensoni* differ from *Gibberula* (type species *G. oryza*) only in size and very minor, species-level shell characters. *Granula* was synonymized under *Gibberula* by Cossmann (1899:96) and Wenz (1943:141). *Kogomea*, likewise differing only in minor characters, was synonymized by Roth and Coan (1971:579) and Rehder (1980:85). *Diluculum* was discussed and synonymized by Kilburn and Rippey (1982:113, 214). Barnard (1962) described *Diluculum* and its type species simply because the radula was known, whereas other species "are merely names given to the shells of molluscs whose anatomy is unknown (op. cit., p. 14)." This is clearly untenable. The wishbone-shaped radula was an error in observation, likewise made by Ponder (1970:70, fig. 3F). This error was discussed in Coovert (1989b:12). Gofas (1989a) correctly figured a number of radulae from *Gibberula*, drawn from SEMs. The five Laseron (1957) genera were all based on species-level characters, and are here synonimized with *Gibberula*. The type species of all these genera show a distinct siphonal notch. The type species of *Phyloginella* was figured by Kaicher (1992: #6211). Powell (1979:222) synonymized *Lataginella* under *Kagomea (sic)*.

Remarks: *Gibberula cucullata* Gofas and Fernandes, 1988, with strongly developed "parapodia," has a highly modified head. The bifurcated tips of the head taper into divergent anterior lobes. These tips can be interpreted as being either the anterior lobes of the head and thus lacking tentacles, or the tentacles themselves and lacking the anterior lobes. Based on the sharply pointed tips and relative position of the eyes, we interpret these tips as being the anterior lobes of the head, the animal lacking tentacles. Gofas and Fernandes (1988:25) suggested that this species "may deserve separate generic status." *Gibberula subbulbosa* (Tate, 1878) (based on unpubl. data ex. R. Burn and D. Hewish) has a similarly constructed head but apparently lacks the strongly developed "parapodia." Until the external anatomy of the type species of all related genus-group names are known, it is considered unwise to place these species in a different genus-level group.

This large, widely distributed group is well characterized by radular, external anatomical, and conchological characters. See *Persicula* for additional discussion.

Genus *Canalispira* Jousseaume, 1875
(figure 49)

Canalispira Jousseaume, 1875:168, 270

Baroginella Laseron, 1957:286–287 [TS: *B. infirma* Laseron, 1957; OD]

Type species: *C. olivellaeformis* Jousseaume, 1875; M (figure 49)

Diagnosis: Shell minute to medium size, white, hyaline, rarely with faint pattern, cylindrical-biconic to obovate or obconic; sutures usually impressed to channeled; spire medium to tall; lip thickened, smooth or lirate; external varix absent; siphonal notch absent; deeply channeled posterior notch present; columella multiplicate with combined total of 3–6 plications + parietal lirae. Modified Type 4 animal; tentacles absent; siphon not visible; foot split anteromedially, covering external shell surface anterolaterally.

Description: Shell (figure 49) minute to medium in size (adult length 2.2–10.3 mm). Color usually white, hyaline, rarely with faint brown maculations, fine oblique lines, or weak axial streaks; surface smooth, glossy. Shape cylindrical-biconic to narrowly obovate or obconic; usually very weakly to weakly shouldered. Sutures distinctly to weakly channeled, deeply impressed, or completely callused over. Spire medium to tall. Aperture narrow to moderately broad, wider anteriorly. Lip moderately thickened, especially posteriorly, thinner anteriorly, outer edge incurved on posterior half, usually weakly to strongly lirate but smooth and lacking lirae in some species, completely lacking an external varix. Shell lacking a siphonal notch but with a sharply, narrowly, and deeply channeled posterior notch. Parietal callus wash usually confined to aperture. Columella multiplicate, with combined total of 3–6 plications + parietal lirae occupying half or more of the aperture length. Shell with cystiscid internal whorls.

External anatomy: 2 species studied. Modified Type 4 animal; tentacles absent; triangular lobes of head pointed anteriorly; the small black eyes medially placed on each triangular lobe; siphon not visible; mantle extension undetermined; foot narrow, about as wide and long as the shell, split anteromedially, covering the anterior end of the shell laterally like "parapodia"; animal white or colorless. (Largely based on unpubl. notes and drawings of an undescribed W. Australian species, ex. P. W. Clover).

Internal anatomy: Unknown.

Radula: 2 species studied. Type 3, uniserial, ribbon long, narrow, composed of 121–136 plates. Rachidian plates overlapping, narrow (0.016–0.033 mm wide), moderately to strongly arched, with 7 sharp cusps on posterior edge. The central cusp is usually the strongest. Anterior edge of rachidian plate strongly concave, resulting in U- or V-shaped plates. Shell length: radular width ratio = 176–270. Radular Index = 17.3–19.4.

Distribution and Habitat: So. Australian (1 species), Indo-Pacific (7 species), W. Atlantic (3 species), South African (2 species). Intertidal to 540 m.

Fossil Record: Pliocene of Australia to Recent.

Nomenclature, Synonymy: The lectotype of *C. olivellaeformis* was figured by Kilburn (1990:fig. 5) and is illustrated here (figure 49). We studied the holotype of *B. infirma* and it is clearly congeneric, differing only in the degree of channeling of the sutures. We regard this character to be of species-level and synonymize *Baroginella* with *Canalispira*.

Remarks: The modified Type 4 animal and lack of a siphonal notch render this group distinct, but the Type 3 radula clearly places this genus in the Persiculini. More study is needed of living animals.

Subfamily GRANULININAE Coovert and Coovert, new subfamily

Diagnosis: Shell minute to small, white, hyaline; surface smooth or sculptured; spire flat to immersed; lip thickened, smooth or denticulate; external varix present; siphonal notch absent; columella with 2 internally reduced columellar plications, plus 1 or 2 pseudo-continuous plications; internal whorls modified cystiscid type. Type 2 animal; tentacles long, slender; siphon moderately long; mantle pustulose, extending over external shell surface; foot long, narrow. Type 4 radula. Internal anatomy unknown.

Genus *Granulina* Jousseaume, 1888 (figures 4, 24, 50)

Granulina Jousseaume, 1888:191
? † *Cryptospira (Cypracolina)* Cerulli-Irelli, 1911:231 [TS: *Voluta clandestina* Brocchi, 1814 †; M]
Merovia Dall, 1921:86 [TS: *Merovia pyriformis* (Carpenter, 1865), = *Volutella pyriformis* Carpenter, 1865, = ? *Marginella margaritula* Carpenter, 1857b; M]
Microginella Laseron, 1957:280 [TS: *Marginella anxia* Hedley, 1909; OD]
Gibberulina auctt., non Monterosato, 1884

Type species: *Marginella pygmaea* Issel, 1869 (*non Marginella pygmaea* G. B. Sowerby II, 1846), = *Marginella isseli* G. & H. Nevill, 1875 (nom. nov.); M (figure 50)

Diagnosis: Shell minute to small, white, hyaline; spire immersed; lip strongly thickened, usually denticulate; external varix present; siphonal notch absent; collabral parietal callus ridge often present; columella with 4 strong plications that are often excavated inside aperture. Type 2 animal; tentacles long, slender; siphon moderately long; foot long, narrow; mantle pustulose, extending over external shell surface.

Description: Shell (figures 4, 50) minute to small (adult length 0.8–3.2 mm). Color white, hyaline; surface smooth, glossy, rarely with fine, weak axial costae or minutely pitted. Shape narrowly to broadly elliptic, obovate, subtriangular, or pyriform; very weakly to weakly shouldered. Spire usually immersed. Aperture narrow to moderately broad, noticeably wider anteriorly and slightly wider posteriorly. Lip moderately to greatly thickened,

especially posteriorly, usually distinctly denticulate, rarely smooth, with distinct external varix. Shell lacking a siphonal notch; posterior notch usually absent, rarely weakly developed. Shell usually with a weak to distinct collabral parietal callus ridge that often intersects columellar plications. Columella with 4 strong plications, third and fourth rarely weak, rarely with weak parietal denticles posterior to plications. Plications often appearing excavated inside aperture due to callus deposits from anterior end of collabral parietal callus ridge. Plications occupying half or less the aperture length. Shell with modified cystiscid internal whorls.

External anatomy: 13 species studied. Type 2 animal, with long, slender tentacles; eyes at base of tentacles; siphon simple, moderately long; mantle pustulose, extending symmetrically over most of external shell surface; foot narrower to slightly wider than shell and about twice the shell length; animal variously marked with tiny dots, spots, or areas of concentrated pigmentation, markings usually black, white, or yellow, but may be orange or turquoise.

Internal anatomy: Unknown.

Radula (figure 24): 12 species studied. Type 4, uniserial, ribbon long, narrow, composed of 90–159 plates. Rachidian plates usually completely non-overlapping, very narrow (0.006–0.012 mm wide), moderately arched, with 9 to 12 raised, clustered denticles located in staggered positions on dorsal surface, with a single (or asymmetrically paired) strong central cusp protruding posteriorly. Anterior edge of rachidian plate weakly concave, resulting in vaguely V-shaped plates. The rachidian plates are asymmetrical and alternate as mirror images. Shell length: radular width ratio = 164–351. Radular Index = 8.2–13.7.

Distribution and Habitat: So. Australian (3 species), Indo-Pacific (13 species), E. Pacific (3 species), W. Atlantic (12 species), Mediterranean (8 species), W. African (3 species), South African (3 species). Intertidal to 1,285 m (single record at 1,700 m).

Fossil Record: Miocene to Pliocene of W. Atlantic, Pliocene of Italy, Pleistocene of Japan and California, to Recent

Nomenclature, Synonymy: The type species and generic synonymy of *Granulina* was discussed in Coovert (1987b). Although the "problem of *Granulina clandestina*" was treated by Gofas (1992:5–6), with a neotype designated and figured (op. cit., fig. 3), several discrepencies remain. Brocchi (1814:642–643, pl. 15, fig. 11) described and figured a shell with 3 columellar plications, a slightly exserted spire, and a pyriform shape. This was considered to be a juvenile by Gofas (1992:5), but juvenile *Granulina* have four plications, an immersed spire, and an ovate or globose shape. More study is needed to resolve these discrepencies. The lectotype of *V. pyriformis*, type species of *Merovia*, was figured by Coan and Roth (1966: pl. 51, fig. 77). Further research is needed to clearly establish the synonymy of this species with *M. margaritula*. We have studied syntypes of *M. anxia*, type species of *Microginella*, and regard them to be referable to *Granulina*.

Remarks: Absence of a siphonal notch and presence of a distinct external varix distinguish this genus from all other cystiscid genera except *Pugnus*. Shell shape and usual lack of sculpturing will further characterize *Granulina*. The very distinct Type 4 radula, modified cystiscid internal whorls, and Type 2 animal clearly distinguish these two genera as a separate subfamily. For a discussion of *G. hadria* (Dall, 1889), see Coovert (1988a).

Genus *Pugnus* Hedley, 1896
(figure 51)

Pugnus Hedley, 1896:105–106
Marginellopsis Bavay, 1911:241 [TS *M. serrei* Bavay, 1911; M]

Type species: *P. parvus* Hedley, 1896; OD (M) (figure 51)

Diagnosis: Shell minute, white, hyaline; surface minutely sculptured; spire flat to immersed; lip thickened, smooth or denticulate; external varix present; siphonal notch absent; columella with 3 or 4 plications. Type 2 animal; tentacles long, slender; siphon moderately long; foot long, narrow; mantle pustulose, extending over external shell surface.

Description: Shell (figure 51) minute (adult length 0.75–2.0 mm). Color white, hyaline; surface sculpture of extremely fine, crossed spiral and axial threads leaving rows of quadrate or hexagonal pits in between, or with spiral or axial rows of beads or short, dashed ridges which are often serpentine or interconnected. Shape broadly cylindrical to broadly subtriangular; weakly to strongly narrowed anteriorly, strongly shouldered. Spire flat to immersed. Aperture moderately narrow to broad, wider anteriorly and slightly wider posteriorly. Lip strongly thickened, especially posteriorly, distinctly denticulate or smooth, with distinct external varix. Shell lacking a siphonal notch and posterior notch. Often with a distinct parietal callus wash extending out of aperture. Columella with 3–4 plications, third and fourth often weak. Plications occupying less than half the aperture length. Shell with modified cystiscid internal whorls.

External anatomy: 1 species studied. Type 2 animal, with long, slender tentacles; eyes at base of tentacles; siphon simple, moderately long; mantle pustulose, extending symmetrically over most of external shell surface; foot narrower than shell and about twice the shell length; animal variously marked with tiny reddish dots and spots on a translucent background. [Based on pers. obs. of photographs of *P. serrei* (Bavay, 1911), ex. Colin Redfern].

Internal anatomy: Unknown.

Radula: 2 species studied. Type 4, uniserial, ribbon long, narrow, of >124 plates. Rachidian plates usually completely non-overlapping, very narrow (0.006 mm wide), moderately arched, with 11–12 raised, clustered denticles located in staggered positions on dorsal surface, with a single (or asymmetrically paired) strong central cusp protruding posteriorly. Anterior edge of rachidian plate weakly concave, resulting in vaguely V-shaped plates. The rachidian plates are asymmetrical and alternate as mirror images. Shell length: radular width ratio = 161–242. Radular Index = 10.3.

Distribution and Habitat: S. Australian (1 species), Indo-Pacific (1 species), W. Atlantic (2 species). Intertidal to 60 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: *Marginellopsis* is here synonymized with *Pugnus* on the basis of very similar radulae (pers. obs. of SEMs, ex. Dean Hewish) and similar shell sculpturing between the type species of the two groups. An undescribed species from Brazil has characters of both groups, and *P. maesae* Roth, 1972 is intermediate in shell shape. Special attention should be paid to the distinctive surface sculpturing uniting them all. These differences are provisionally considered to be of specific value only. See Roth (1972:107) for remarks on differing familial placement.

Remarks: For general comments, see remarks under *Granulina*.

Family MARGINELLIDAE Fleming, 1828:328

Diagnosis: Shell minute to very large, white, uniformly colored, or patterned; protoconch paucispiral; lip thickened, smooth or denticulate; external varix present or absent; siphonal notch present or absent; columella with 2–6 plications; internal whorls unmodified type. Type 1 or Type 2 animal; operculum absent. Marginellid radula, Type 5, 6, modified Type 6, Type 7, 8, or 9, or non-radulate. Mantle cavity with monopectinate ctenidium and bipectinate osphradium. Proboscis pleurembolic; jaws absent; marginellid buccal pouch present, absent in non-radulate species; odontophoral cartilages fused anteriorly or both anteriorly and posteriorly; valve of Leiblein present or absent, with or without bypass tube; esophageal caecum present or absent; gland of Leiblein large, sacculate, and emptying directly into posterior end of esophagus, or with long, convoluted duct and a terminal bulb, emptying either into posterior end of esophagus or passing through nerve ring and emptying into anterior end of proboscis; paired salivary glands aseinous or tubular, either attached to esophagus just anterior to the valve of Leiblein, contained within proboscis, or free, ducts either embedded in or attached to walls of esophagus, or free; single accessory salivary gland present or absent, aseinous or tubular; anal gland present.

Remarks: We currently recognize a total of 483 species in the Marginellidae, of which 51 remain to be described. The two subfamilies were recognized in Coan (1965) but were not clearly based on anatomical characters.

Key to the Recent Genera of the Family Marginellidae

1a. Adult shell very large, over 50 mm in length; siphonal notch present, broad, weak to distinct; spire medium height, with large, often somewhat bulbous protoconch; lip narrowly thickened, smooth, without denticulation 2

1b. Adult shell minute to large, rarely very large, if over 50 mm, then spire immersed or with strongly thickened, denticulate lip; spire immersed to tall, protoconch not unusually large; lip narrowly to strongly thickened, with or without denticulation 3

2a. Columella with 4 very strong, nearly transverse plications; 1st plication well posterior of anterior border of columella; with very distinct parietal callus deposit posteriorly; shell often somewhat dull and crazed or blistered ..... *Afrivoluta*

2b. Columella with 2 strong, very oblique plications; 1st plication bordering anterior end of columella; without distinct parietal callus deposits; shell very smooth, glossy ... *Marginellona*

3a. Columella with 4 strong plications occupying more than half the aperture length; if with weak "false 5th" plication, then with distinct posterior notch; spire low, medium, or tall; external varix distinct; often with weak to distinct siphonal notch present 4

3b. Columella with 2–6 plications, those with 4 or fewer plications occupying half or less the aperture length; spire immersed, or low, medium, or tall; external varix distinct, weak, or absent; siphonal notch usually absent, if present, with more than 4 plications 12

4a. Shell with distinct to weak siphonal notch 5

4b. Shell completely lacking a siphonal notch, the anterior end rounded, or notch very weak and obscure 8

5a. Shell usually white or uniformly colored yellowish-white to yellowish-orange, rarely with several obscure pale yellow spiral bands; Australian or Neozelanic distribution 6

5b. Shell usually with distinct and colorful pattern of spots or dots, numerous spiral lines, mottled, or with axial streaks or lines, or various combinations; eastern Atlantic or western Indian Ocean distribution 7

6a. Posterior notch present, sharply defined; lip rapidly thickening posteriorly, narrowed slightly then widening again at posterior ¼; lip smooth, not denticulate; body whorl generally pyriform, strongly narrowed at anterior ¼; usually with heavy ventral callusing; spire whorls convex or shouldered, giving uneven profile; posterior end

of lip joins body whorl well below suture above; 4th plication not distinctly remote .. *Austroginella*

6b. Posterior notch weak to absent; lip thickest medially, uniformly thickened throughout; lip smooth or weakly denticulate; body whorl obovate, usually straight to convex at anterior ¼; spire whorls evenly contoured, essentially straight in profile; posterior end of lip joins body whorl at or slightly below previous suture; 4th plication often remote (i.e. farther separated than other 3) ..... *Mesoginella*

7a. Shell with distinct to obscure axial costae; aperture usually broadest medially; lip strongly denticulate ..... *Glabella*

7b. Shell smooth, completely lacking axial costae; aperture usually broadest anteriorly; lip smooth or denticulate ..... *Marginella* (part)

8a. Lip flared at shoulder, weakly to strongly alate; shell usually strongly narrowed anteriorly 9

8b. Lip not notably flared or alate; shell not usually strongly narrowed anteriorly 10

9a. With a strongly marked posterior notch in corner of aperture; columellar plications appear excavated inside aperture due to callus deposits; weak "false 5th" plication present; lip strongly thickened, with distinct denticulation ..... *Protoginella*

9b. With at most a weak, broadly rounded posterior notch in corner of aperture; columellar plications rounded, not appearing excavated inside aperture; lacking "false 5th" plication; lip moderately thickened, usually lacking denticulation, if present, usually weak ..... *Alaginella*

10a. Shell either with intricate pattern of spiral and axial elements, or shell length > 15 mm ..... *Marginella* (part)

10b. Shell usually white or uniformly colored; pattern, if present, consisting of only 1 to 4 narrow spiral bands; shell minute to medium in size, 1.9–12.0 mm in length 11

11a. Labial denticulation always present, subequal throughout; spire low to medium height; shell broadly obconic in shape; some species with weak to distinct axial costae ..... *Eratoidea*

11b. Labial denticulation sometimes absent, if present, with either a single strong posterior labial denticle, or posterior denticle distinctly stronger than others; spire medium to tall; shell usually narrowly biconic, rarely broadly biconic in shape; rarely with axial costae ..... *Dentimargo*

12a. Spire immersed or nearly so 13

12b. Spire low to medium 20

13a. External varix extremely weak to absent; columella with 3 plications; shape narrowly cylindrical ..... *Volvarina* (part)

13b. External varix strong, distinct, if weak to absent, then with 4 columellar plications; columella with 3–6 plications; shape various 14

14a. Columella with 3 plications that are crowded anteriorly; shape cylindrical to narrowly obovate 15

14b. Columella with 4–6 plications, that often occupy half or more the aperture length; shape broadly elliptic to obovate, rarely cylindrical to narrowly obovate 16

15a. Without labial denticulation; body whorl usually somewhat abruptly narrowed anteriorly ..... *Balanetta*

15b. With fine labial denticulation in adult; body whorl gradually narrowed anteriorly ..... *Hydroginella* (part)

16a. Columella with 4, 5, or 6 plications; if with only 4 plications, then lip completely lacking denticulation, shell uniformly colored or patterned, and shell moderately large to large ..... *Cryptospira* (part)

16b. Columella with 4 plications; lip usually distinctly denticulate; if not denticulate, then shell white, and small to medium in size 17

17a. Columellar plications usually thin, sharp, anteriorly crowded; if not, then lacking labial denticulation; Indo-Pacific distribution 18

17b. Columellar plications thick, moderately heavy, not crowded anteriorly; western Atlantic distribution 19

18a. Labial denticulation strong, distinct; shell usually with distinct color, lip and apical spot darker, rarely grayish-white; columella with 4 thin, sharp, anteriorly crowded plications; western Indian Ocean distribution ..... *Closia*

18b. Labial denticulation usually absent, rarely weakly developed; shell white, lacking coloration; columella with 4 thin to moderately heavy plications occupying less than half the aperture length, crowded anteriorly in some; Australian or Neozelanic distribution ..... *Ovaginella*

19a. Shell white; unpatterned or with 2 obscure, broken spiral bands ..... *Prunum* (part)

19b. Shell distinctly colored; distinctly patterned with spots or numerous spiral bands ..... *Bullata*

20a. Columella with 3 plications that are crowded anteriorly; weak to strong collabral parietal callus ridge present posterior to plications, the posterior end often appearing as "false 4th" plication; lip with fine denticulation.. *Hydroginella*

20b. Columella with 2–6 plications that are not crowded anteriorly; usually lacking collabral parietal callus ridge; if present, then lip not denticulate, or with 2nd collabral callus ridge inside aperture and 4 plications; lip with or without denticulation, if present, usually strong 21

21a. Columella with 5–6 continuous plications; shell usually solid gray, or gray with spiral lines or a distinct pattern of spiral lines interrupted by longitudinal streaks, but not white and unmarked; spire low, depressed; shell broadly elliptic, obovate, pyriform, or subtriangular; me-

dium-sized to large, length 6.2–46.0 mm; Indo-Pacific distribution ..... *Cryptospira* (part)

21b. Columella with 2–4 plications; if with more than 4 plications, then either (1) with a "false 5th" plication and shell narrow and cylindrical, (2) color pure white, opaque, with a weak siphonal notch, or (3) western Atlantic distribution; otherwise not as above 22

22a. Siphonal notch weak but present; Indo-Pacific, Australian, or Neozelanic distribution 23

22b. Siphonal notch completely absent; if weak but present, then West African distribution; widely distributed 24

23a. Columella with 4 plications, 4th plication often remote; shell translucent white to white, without heavy ventral callus deposits; with distinct external varix; Australian or Neozelanic distribution ..... *Mesoginella* (part)

23b. Columella with 5–6 plications; shell opaque milky white with heavy ventral callus deposits; with or without external varix; Indo-Pacific distribution ..... *Volvarina* (part-*monilis* Group)

24a. With "false 5th" plication present as a transverse denticle or weak parietal lira, neither extending into aperture appreciably, rarely absent; lip denticulate when fully adult; shell cylindrical or subcylindical; distinct external varix present; shell colored and multi-banded or white; Indo-Pacific, Australian, or Neozelanic distribution ..... *Serrata*

24b. With 4 columellar plications; if 5th present, then continuous, not a "false 5th" or weak parietal lira; lip smooth or denticulate; shell variously shaped; if cylindrical or subcylindrical, then lip smooth, not denticulate; distinct external varix present or absent; widespread distribution 25

25a. Collabral parietal callus ridge present, although often weak, plus a collabral callus ridge present inside aperture, both just posterior to 4 strong columellar plications; lip with strong denticulation; external varix present, lip moderately to strongly thickened, especially at anterior third; shape obovate to subpyriform; color translucent white or light orange; East African distribution ..... *Serrataginella*

25b. Lacking collabral callus ridge inside aperture; if collabral parietal callus ridge present, then with only 3 columellar plications and lip smooth; otherwise lacking above combination of characters 26

26a. Columellar plications 2, 3, or 4, thin and sharp; shell very thin, translucent or hyaline, color white to amber, usually unpatterned, rarely with faint yellowish-white spiral bands; external varix absent, if present, very weak; lip smooth, completely lacking denticulation ..... *Hyalina*

26b. Columellar plications 3, 4, or 5, not unusually thin and sharp; if only 3, then joined by short collabral callus ridge posteriorly; shell color various, shell often thicker, not unusually thin and translucent; external varix present or absent, if absent, columellar plications thicker; labial denticulation present or absent 27

27a. Shell with ventral and apical callus wash minutely granulated; with distinct external varix; lip smooth, lacking denticulation; aperture broad; freshwater, SE Asian distribution ..... *Rivomarginella*

27b. Shell lacking minute granulations ventrally and apically; without above combination of characters; not freshwater, widely distributed 28

28a. Labial denticulation present in many species, but may be absent; color uniformly white, cream, or gray, or spotted to streaked in some, but generally not with narrow darker bands alone (bands, if present, of pale background color interrupting darker shell color); columella with 4–5 plications; heavy ventral callusing common, especially callus pad near posterior commissure of lip; if shell white and lacking labial denticulation, then unpatterned, with 4 columellar plications, and western Atlantic distribution ..... *Prunum*

28b. Labial denticulation absent; color translucent white to orange or brown, usually with yellow, orange, brown, or reddish-brown narrow bands, which are darker than shell color, rarely axially streaked, not patterned with spots; columella with 3–4 plications; ventral callus deposits weak or absent ..... *Volvarina* (part)

Subfamily MARGINELLONINAE Coan, 1965:186, 191

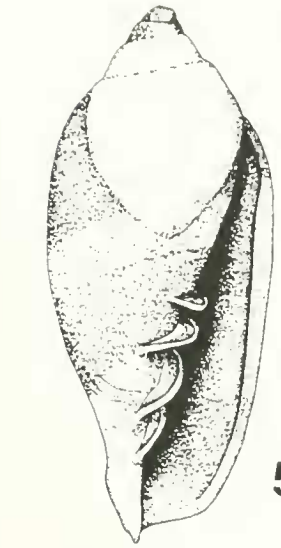
Diagnosis: Shell very large; spire medium height; protoconch large; lip narrowly thickened, smooth, lacking denticulation; external varix present; siphonal notch present; columella with 2 or 4 strong plications. Type 1 animal; tentacles relatively short; eyes reduced or absent; siphon moderately long. Type 7 radula. Marginellid buccal pouch present; valve of Leiblein present, without bypass tube; esophageal caecum absent; gland of Leiblein large, sacculate, emptying directly into posterior end of esophagus; paired salivary glands tubular, free, ducts free along floor of proboscis; single accessory salivary gland absent.

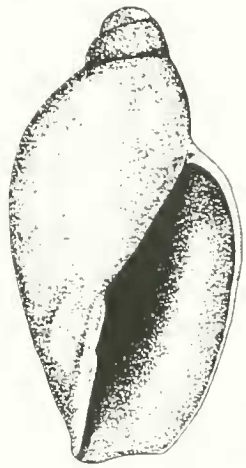
Genus *Afrivoluta* Tomlin, 1947
(figures 5, 6, 52)

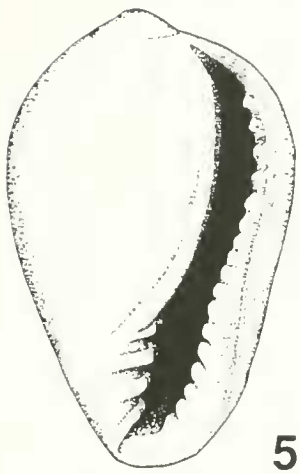
Afrivoluta Tomlin, 1947:244

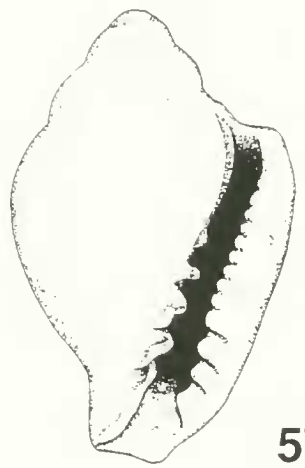
Type species: *A. pringlei* Tomlin, 1947; OD (M) (figure 52).

Diagnosis: Shell very large, volute-shaped; spire medium height; protoconch large; lip narrowly thickened, smooth, lacking denticulation; external varix present; broad, distinct siphonal notch present; distinct parietal callus deposit present; columella with 4 strong, nearly









Figures 52–60. Shells of type species of marginellid genera, ventral views. **52.** *Afrivoluta pringlei* Tomlin, 1947. GAC M1819, Agulhas Bank, South Africa, trawled at 110 m. Length 115.4 mm. **53.** *Marginellona gigas* (Martens, 1904). Holotype of *Sigaluta pratasensis* Rehder, 1967, USNM 237018, W. of Pratas Reef, South China Sea, 20°37'N, 115°43'E, in 380 m, gray mud and sand bottom. After photos in Harasewych and Kantor (1991 fig. 2) and Weaver and DuPont (1970 pl. 10, fig. H, I). Length 54.1 mm.

transverse plications, 1st plication beginning well posterior of anterior end of columella. Type 1 animal; tentacles relatively short; eyes reduced; siphon moderately long; mantle smooth, extending at least partially over external shell surface.

Description: Shell (figure 52) very large (adult length 84.7–130.9 mm). Color tawny to cinnamon or pinkish-tan. Relatively thin-shelled, surface smooth and semi-glossy with evident growth lines, often crazed or with weak to distinct bubbles or blisters in shell surface. Shape oblong, volute-shaped, broadest at about posterior third, narrowed anteriorly, very weakly shouldered. Spire of medium height, apex swollen, blunt. Aperture broad, wider anteriorly. Lip narrowly thickened inside and rolled externally, producing a distinct external varix with a sharp dorsal margin unconnected to 1st columellar plication. Lip smooth, not denticulate. Siphonal notch broad, distinct; posterior notch poorly defined. Parietal callus deposit near posterior commissure of lip large to moderately large. Columella with 4 very strong continuous plications that are nearly transverse to axis, 1st plication beginning well posterior of anterior end. Plications occupying slightly more than half the aperture length. Internal whorls unmodified.

External anatomy (figures 5, 6): 1 species studied. Type 1 animal; tentacles relatively short; eyes very reduced, red, on lateral lappets close to edge; siphon moderately long; mantle smooth, able to extend over at least anterior left half of external shell surface; foot broad, about 2 X shell width, slightly longer than shell, with posteromedial mound corresponding to parietal callus deposit of shell; animal uniformly colored yellowish-tan. (Based on published data, summarized in Coovert, 1987a and Coovert, 1987g:9; plus personal observations of photographs ex. W. R. Liltved).

Internal anatomy: Unknown.

Radula: 1 species studied. Type 7, uniserial, ribbon short, very broad, composed of 70–80 plates. Rachidian plates overlapping, very broad (1.75–1.90 mm wide), nearly flat, with numerous (70–80) sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 61. Radular Index = 0.8.

Distribution and Habitat: South African (1 species). Recorded from depths of 70 to 500 m. Specimens obtained by commercial bottom trawlers.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: The type species and genus were discussed by Coovert (1987a). The holotype was figured by Tomlin (1947:244) and Bruggen (1963:fig. 1).

Remarks: This monotypic genus was discussed by Coovert (1987a, 1987e). The genus was correctly assigned to the Marginellidae by Barnard (1963). The type species has a very large, striking shell. The 4 massive columellar plications are distinctive, with the first situated well posterior of the anterior border of the columella. The very prominent posterior parietal callus deposit is characteristic.

Genus *Marginellona* Martens, 1904
(figures 28, 53, 80)

Marginella (Marginellona) Martens, 1904:108
Sigaluta Rehder, 1967:182–183 [TS: *S. pratasensis* Rehder, 1967, = *Marginellona gigas* Martens, 1904, OD]

Type species: *Marginella (M.) gigas* Martens, 1904; M (figure 53)

Diagnosis: Shell very large, smooth and very glossy, narrowly obovate; spire medium height with shouldered whorls; protoconch large; lip narrowly thickened, smooth, lacking denticulation; external varix apparently present; a broad, weak siphonal notch present; lacking parietal callus deposit; columella with 2 strong, very oblique plications, 1st plication bordering anterior end of columella. Type 1 animal; tentacles relatively short; eyes absent; siphon moderately long.

Description: Shell (figure 53) very large (adult length 53.9–157.0 mm). Color translucent tan, yellowish-brown, or greenish-brown, aperture darker brown. Thin-shelled, surface smooth and very glossy. Shape narrowly obovate, weakly shouldered. Spire medium height, with large bulbous protoconch and shouldered whorls, sutures callused over. Aperture very broad, wider and truncate anteriorly. Lip narrowly thickened, smooth, not denticulate, apparently with a narrow external varix. Siphonal notch very broad, weak; posterior notch poorly defined. Shell with a thin parietal callus wash but no large callus deposits. Columella with 2 strong, nearly axially oriented continuous plications occupying slightly less than half the aperture length. Internal whorls unmodified.

External anatomy: 1 species studied. Type 1 animal; tentacles relatively short; eyes absent; siphon moderately

←

54. *Serrata serrata* (Gaskoin, 1849). Holotype, BM(NH), Mauritius. After photograph in Kaicher (1981:#2690). Length 8.9 mm **55.** *Serrataginella spryi* (Clover, 1974). Holotype, BM(NH) 1973.83, 240 km S of Porto Amelia, Mozambique, low tide under stones. After photos in Clover (1974:fig. 6) and Kaicher (1981:#2629). Length 9.5 mm **56.** *Hydroginella dispersa* Laseron, 1957. Holotype, AMS 103353, Murray Island, Torres Strait, north Queensland, 4–15 m. Length 5.1 mm **57.** *Protoginella lavigata* (Brazier, 1877). Syntype, Katow, New Guinea, mud bottom 13 m. After Hedley (1901 pl. 16, fig. 5). Length 6.4 mm. **58.** *Alaginella oehraeea* (Angas, 1871). GAC Acc. # 28–89, Little Bay, New South Wales. Length 3.5 mm. **59.** *Austroginella muscaria* (Lamarck, 1822). GAC M1232, Victoria, Australia, on beach. Length 15.3 mm **60.** *Mesoginella turbinata* (G. B. Sowerby II, 1846). GAC M1655, Port Stephens, New South Wales. Length 7.2 mm.

long; mantle extension undetermined; foot broad, about 2 X shell width, slightly longer than shell (Harasewych and Kantor, 1991:10).

Internal anatomy (figure 80): 1 species studied. Same as for subfamily.

Radula (figure 28): 1 species studied. Type 7, uniserial, ribbon short, very broad, composed of 56–80 plates. Rachidian plates overlapping, very broad (1.6–2.5 mm wide), nearly flat, with numerous (58–85) sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 43–63. Radular Index = 0.9–1.0.

Distribution and Habitat: Indo-Pacific (1 species). Occurs from the eastern Indian Ocean off the Nicobar Islands and the South China Sea. Recorded from depths of 380 to 1,280 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: The type species of *Sigaluta* is a synonym of *M. gigas*, the type species of *Marginellona*, thus synonymizing these two groups. See discussion in Harasewych and Kantor (1991). The holotype of *Sigaluta pratasensis* is figured herein (figure 53) and in color in Weaver and DuPont (1970:pl. 40, figs. H, I) and Abbott and Dance (1982:220).

Remarks: Harasewych and Kantor (1991) reviewed this monotypic genus. This is the largest marginellid known. The smooth and very glossy shell, 2 very oblique columellar plications, and lack of a parietal callus deposit serve to separate the type species from *Afrivoluta pringlei*, the only marginellid species with which it is likely to be confused.

Subfamily MARGINELLINAE Fleming, 1828:328

Diagnosis: Shell minute to very large, white, uniformly colored, or patterned; lip thickened, smooth or denticulate; external varix present or absent; siphonal notch present or absent; columella with 2–6 plications. Type 2 animal; tentacles long to very long, slender; eyes at base of tentacles on slight swelling; siphon moderately to very long; mantle smooth, pustulose, or papillose, usually at least partially extending over external shell surface. Type 5, 6, modified Type 6, Type 8, or 9 radula, or non-radulate. Marginellid buccal pouch present, absent in non-radulate species; odontophoral cartilages fused anteriorly or both anteriorly and posteriorly; valve of Leiblein present or absent, if present, with bypass tube; esophageal caecum present or absent; gland of Leiblein with long, convoluted duct and a terminal bulb, emptying either into posterior end of esophagus or passing through nerve ring and emptying into anterior end of proboscis; paired salivary glands ascinous or tubular, either attached to esophagus just anterior to the valve of Leiblein, contained within proboscis, or free, ducts either embedded or attached to walls of esophagus, or free; single accessory salivary gland present or absent, ascinous or tubular.

† Genus *Myobarum* Sohl, 1963

Myobarum Sohl, 1963:750–751

Type species: *M. laevigatum* Sohl, 1963 †; OD (M)

Diagnosis: Shell moderately large, surface smooth, glossy; spire medium to tall; sutures callused over; aperture broad; lip thickened, smooth; external varix weakly developed; weak siphonal notch present; strong, narrow posterior notch present; columella with 2 widely-spaced plications, the anterior one bordering the anterior end of the columella.

Fossil Record: Late Cretaceous (Upper Maestrichtian) of Mississippi and Georgia.

Nomenclature, Synonymy: Photographs of the holotype were figured in Sohl (1963:pl. 90, figs. 19, 20) and Sohl (1964:pl. 44, figs. 15, 16).

Remarks: Apparently monotypic. The two widely-spaced columellar plications are unusual. Although originally placed in the Volutidae, Ponder (1973:331) suggested that this genus might belong in the Marginellidae. Petuch and Sargent (1986:10) mentioned *Myobarum* as a possible ancestor to the Olividae. The general shell shape, glossy, callused surface, anterior plication bordering the anterior end of the columella, and the blunt, paucispiral protoconch all indicate a marginellid. Based on these conchological features, this genus is here included in the Marginellidae, subfamily Marginellinae. Placement to tribe must await further, extensive study of the fossil fauna.

Tribe AUSTROGINELLINI Coovert and Coovert, new tribe

Diagnosis: Shell minute to moderately large, white, rarely lightly colored or obscurely banded; spire immersed to tall; lip thickened, smooth or denticulate; external varix present; siphonal notch weak or absent; columella with 2–4 plications occupying more than half to less than half the aperture; some species with a "false 4th" or "false 5th" plication. Type 2 animal; siphon moderately long to very long; mantle smooth, pustulose, or papillose, extending over external shell surface. Type 5, modified Type 6, or Type 8 or 9 radula. Marginellid buccal pouch present; odontophoral cartilages fused anteriorly; valve of Leiblein present, with bypass tube; esophageal caecum absent; gland of Leiblein with a terminal bulb and a long, convoluted duct emptying into posterior end of esophagus; paired salivary glands tubular, attached to esophagus just anterior to the valve of Leiblein, ducts embedded in walls of esophagus; single tubular accessory salivary gland present or absent.

"*Serrata* Group"

Diagnosis: Shell small to medium, white to translucent, uniformly colored or banded in some species; spire immersed or low to medium; lip thickened, finely to coarsely denticulate, rarely smooth; external varix present; siphonal noteh absent; some species with collabral parietal callus ridge; columella with 3 or 4 plications occupying less than half the aperture length, often with "false 4th" or "false 5th" plications. Type 2 animal; siphon moderately long; mantle smooth or pustulose, extending over external shell surface. Modified Type 6, or Type 8 or 9 radula. Anatomy as in tribe, single tubular accessory salivary gland present.

† Genus *Conuginella* Laseron, 1957

Conuginella Laseron, 1957:288

Type species: *Marginella inermis* Tate, 1878 †; OD (M)

Diagnosis: Shell medium size, conical, strongly but evenly narrowed anteriorly; spire low; lip narrowly thickened, denticulate, produced or angulate posteriorly; external varix present; siphonal noteh absent; columella with 4 plications occupying less than half the aperture length.

Fossil Record: Miocene of Australia.

Nomenclature, Synonymy: This group was placed by Coan (1965:190) as a subgenus of *Serrata*.

Remarks: Related to *Exiginella*, a fossil group synonymized below with *Serrata*. *Conuginella* differs in having only 4 columellar plications, a distinctive conical shape, and a produced posterior corner of the lip. Shared features are the presence of an external varix, denticulate lip, and slender shell shape.

Genus *Serrata* Jousseaume, 1875
(figures 26, 54)

Serrata Jousseaume, 1875:167, 230
Haloginella Laseron, 1957:284 [TS. *Marginella mustelina* (Angas, 1871), = *Hyalina (Volvarina) mustelina* Angas, 1871; OD]
† *Exiginella* Laseron, 1957:289 [TS. *Marginella wintei* Tate, 1878 †; OD]

Type species: *Serrata serrata* (Gaskoin, 1849), = *Marginella serrata* Gaskoin, 1849; T (figure 54)

Diagnosis: Shell small to medium, white to brown, often banded, usually cylindrical; spire low to medium; lip thickened, finely to coarsely denticulate, rarely smooth; external varix present; lacking a siphonal noteh; lacking parietal callus deposits and ridge; columella with 4 strong plications plus a weak "false 5th" occupying less than half the aperture length. Type 2 animal; siphon moderately long; mantle smooth or pustulose, extending over external shell surface. Modified Type 6 radula.

Description: Shell (figure 54) small to medium in size (adult length 3.6–13.0 mm). Color white to grayish-white or brown, often with prominent brown spiral bands, or rarely pale orangish-yellow bands; surface smooth, glossy. Shape cylindrical to narrowly elliptic, narrowly subpyriform in one species; weakly to strongly shouldered. Spire low to medium height, rarely very low and obscure. Aperture narrow, usually wider anteriorly. Lip weakly to strongly thickened, finely to coarsely denticulate, rarely smooth, with a weak to distinct external varix. Shell without a siphonal noteh or a posterior notch. Shell with a thin parietal callus wash, lacking large callus deposits and collabral parietal callus ridge. Columella with 4 strong, continuous plications, plus a weak to strong parietal lira or "false 5th" plication, which combined occupy slightly less than half, but more than one-third, the aperture length. Internal whorls presumed unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon moderately long; mantle smooth or pustulose, covering shell symmetrically; foot slightly wider than shell, about 1½ X shell length; animal colored with cream, orange, or buff. See summary in Coovert (1987g:13, 20) as *Haloginella*.

Internal anatomy: 1 species studied. Same as for "*Serrata* Group."

Radula (figure 26): 8 species studied. Modified Type 6, uniserial, ribbon short, broad, of 13–35 plates. Rachidian plates overlapping, thin, fragile, broad (0.052–0.120 mm wide), nearly flat, with numerous (22–59) sharp cusps along sinuous posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 59–117. Radular Index = 0.4–1.6.

Distribution and Habitat: Neozelanic (2 species), S. Australian (7 species), Indo-Pacific (3 species). Intertidal to 370 m.

Fossil Record: Middle Oligocene of New Zealand (*fide* Powell, 1979:217), Miocene of Australia, to Recent.

Nomenclature, Synonymy: The type of *M. serrata* is figured by Kaicher (1981:#2690) and herein (figure 54). Synonymy of *Serrata* and *Haloginella* is based on radular and conchological similarities. The radula of Australian *S. mustelina*, type species of *Haloginella*, has been studied (pers. obs. of SEMs, ex. Dean Hewish) and compared with radulae from *S. translata* (Redfield, 1870), an undoubted congener of *S. serrata*, type species of *Serrata*. These radulae and shells compare very favorably, and the generic groups they represent are herein considered synonyms. For discussion of *Haloginella*, see Coovert (1987f). *Exiginella* is synonymized based on conchological similarity to the other two groups, including a fairly strong 5th columellar plication, denticulate lip, and an external varix.

Remarks: *Haloginella* and *Serrata* had been considered distinct until we extracted radulae of *S. translata*. The

shared possession of a modified Type 6 radula, shell with a weak "false 5th" plication, lack of a collabral parietal callus ridge, and the usually denticulate lip are diagnostic. Coan (1965:190) considered *Haloginella* a subgenus of *Volvarina* and was subsequently followed by others. Anatomical features described by Ponder (1970) clearly place this group, along with *Mesoginella* and *Austroginella*, in a separate tribe, based especially on the presence of a valve of Leiblein, the absence of an esophageal caecum, and the emptying of the duct from the gland of Leiblein into the esophagus posterior to the nerve ring.

Genus *Serrataginella* Coovert and Coovert, new genus
(figures 29, 55)

Type species: "*Marginella*" *spryi* Clover, 1974; OD (M), herein (figure 55)

Diagnosis: Shell medium-sized, translucent white to light orange, unbanded, broadly obovate to subpyriform; spire low; lip strongly thickened, coarsely denticulate; external varix present; lacking a siphonal notch; with collabral parietal callus ridge plus parallel callus ridge inside aperture; columella with 4 strong plications occupying about one-third the aperture length, lacking "false 5th" plication. Type 8 radula.

Description: Shell (figure 55) medium in size (adult length 8.0–9.9 mm). Color translucent white to light orange; surface smooth, glossy. Shape broadly obovate to subpyriform, moderately strongly shouldered. Spire low. Aperture narrow, usually wider anteriorly, narrowest medially due to incurving of lip. Lip moderately to strongly thickened, especially anterior third, coarsely denticulate in adults, denticulation absent in subadults, first developing anteriorly, with a strong external varix. Siphonal notch absent; posterior notch absent. Shell with a weak but distinct collabral parietal callus ridge just outside aperture, plus weak to distinct collabral callus ridge well within aperture, both most distinct just posterior to plications. Columella with 4 strong, continuous plications, lacking parietal lira or "false 5th" plication. Plications occupying about ⅓ aperture length. Internal whorls presumed unmodified.

External anatomy: 1 species studied. Animal reported to be light orange in color (Clover, 1974:215).

Internal anatomy: Unknown.

Radula (figure 29): 1 species studied. Type 8, uniserial, ribbon short, broad, of 38 plates. Rachidian plates overlapping, broad (0.191 mm wide), nearly flat, with 9–10 sharp cusps along posterior edge. The entire posterior edge, including all of the edges of the main cusps, with numerous (total of ca. 70) small, subordinate cusps, giving the main cusps a serrated appearance. Anterior edge of rachidian plate slightly indented medially, resulting in a very shallowly V-shaped plate. Shell length: radular width ratio = 42. Radular Index = 4.0.

Distribution and Habitat: Indo-Pacific (1 species). Recorded from E. African coast. Intertidal to 30 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: A photograph of the holotype of the type species was figured by Clover (1974:pl. 8, fig. 6) and Kaicher (1981:#2629). Name derived from *Serrata*, valid marginellid genus to which this new genus is believed to be allied, and L. *serrata*, toothed like a saw, serrated, in reference to the serrated cusps of the radula, combined with *-ginella*, adopted from *Marginella*. Gender feminine.

Remarks: This monotypic genus is characterized by the very distinctive radula, possession of a collabral callus ridge on the parietal area as well as inside the aperture, plus the 4 strong columellar plications and strong labial denticulation. Placement is based on conchological similarities to *Serrata* and *Hydroginella*. See Coomans (1975) for further information. See Key for further differentiation.

† Genus *Strombogincella* Laseron, 1957

Strombogincella Laseron, 1957:289

Type species: *Marginella crassidens* Chapman and Crespin, 1928 †; OD (M)

Diagnosis: Shell medium size, broadly biconic, strongly narrowed and acute anteriorly; spire medium height; aperture very narrow; lip thickened, denticulate; external varix present; siphonal notch absent; columella with 4 plications crowded anteriorly.

Fossil Record: Pleistocene of Australia.

Nomenclature, Synonymy: Coan (1965:189) placed this group as a subgenus of *Marginella*, but the anteriorly crowded plications indicate little relationship.

Remarks: The broadly biconic shell shape strongly narrowing anteriorly and the very narrow aperture are apparently unique features of this monotypic genus. The denticulate lip and general shape indicate placement in Austroginellini, "*Serrata* Group," whereas the 4 anteriorly crowded plications indicate close relationship to *Hydroginella*.

Genus *Hydroginella* Laseron, 1957
(figures 30, 56)

Hydroginella Laseron, 1957:284
Neptoginella Laseron, 1957:283 [TS *N. fascicula* Laseron, 1957; OD]
Pillarginella Gabriel, 1962:197 [TS *Marginella columnaria* Hedley & May, 1908; OD (M)]

Type species: *H. dispersa* Laseron, 1957; OD (M) (figure 56)

Diagnosis: Shell small to medium, white to orangish-brown or amber, hyaline or translucent, rarely banded,

usually cylindrical, obovate, or subpyriform; spire immersed or low to medium; lip thickened, usually finely denticulate, rarely smooth; external varix present; lacking a siphonal notch, collabral parietal callus ridge usually present; columella with 3 plications plus a weak "false 4th" occupying less than ¼ the aperture length. Type 2 animal; siphon moderately long; mantle extension undetermined. Type 9 radula.

Description: Shell (figure 56) small to medium (adult length 3.0–10.3 mm). Color white to orangish-brown to amber, hyaline or translucent, one species with 3 broad pale orange spiral bands; surface smooth, glossy. Shape narrowly to broadly cylindrical or obovate to subpyriform, usually strongly narrowed anteriorly; weakly to strongly shouldered. Spire immersed or low to medium height. Aperture usually narrow throughout, some species moderately broad, often wider anteriorly or narrowest medially due to incurved lip. Lip moderately to strongly thickened, thickest medially or at anterior third, usually finely denticulate in adults, denticulation often weak or absent medially, rarely completely absent, with weak to strong external varix. Siphonal notch absent; posterior notch absent. Shell with weak to strong collabral parietal callus ridge beginning just posterior to plications, appearing at that point as "false 4th" plication, ridge rarely absent. Columella with 3 continuous plications crowded anteriorly, occupying ¼ or less of aperture length. Internal whorls unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon moderately long; mantle extension undetermined; foot about as wide as shell, slightly longer, some species with opaque white spots. See Bouchet (1989:79, fig. 2).

Internal anatomy: Unknown.

Radula (figure 30): 4 species studied. Type 9, uniserial, ribbon very short, narrow, greatly reduced, of 10–30 plates. Rachidian plates weak, overlapping, narrow (0.019–0.032 mm wide), nearly flat, with few (4–7) cusps along posterior edge. Anterior edge of rachidian plate straight, resulting in subquadrate plates. Shell length: radular width ratio = 230–391. Radular Index = 2.3–7.5.

Distribution and Habitat: S. Australian (4 species), Indo-Pacific (13 species). Intertidal to 550 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: Bouchet (1989) discussed *Hydroginella* and *Neptoginella* and figured the holotypes of both type species (note that his captions of figs. d and e were reversed). Although conchological similarities were discussed, these genera were not synonymized. These groups, plus *Pillarginella*, are here considered congeneric based on distinctive conchological features, especially the presence of a collabral parietal callus ridge and only 3 columellar plications. The very distinctive radula is known from four species (Bouchet, 1989:fig. 3; Hewish, 1990:fig. 2A), including *H. columnaria* (pers. obs. of SEMs, ex. Dean Hewish), the type species of *Pillarginella*. The principle of first reviser (ICZN Art. 24) is employed in choosing *Hydroginella* over *Neptoginella*. These 3 groups form a very distinctive assemblage of species.

Remarks: Bouchet (1989) reported on the parasitism of sleeping fish by *H. caledonica* (Jousseaume, 1877). The very unusual, highly reduced radula, characteristic of this group, suggests a similar behavior in the other species.

"*Austroginella* Group"

Diagnosis: Shell minute to moderately large, white, rarely lightly colored or obscurely banded; spire immersed to tall; lip thickened, smooth or denticulate; external varix present; siphonal notch weak or absent; columella with 2–4 plications occupying more than half to less than half the aperture, some species with a "false 5th" plication. Type 2 animal; siphon long to very long; mantle smooth, weakly pustulose, or papillose, extending over external shell surface. Type 5 radula. Anatomy as in tribe, single accessory salivary gland absent.

† Genus *Mioginella* Laseron, 1957

Mioginella Laseron, 1957:287

Type species: *Marginella regula* Cotton, 1949 †; OD (M)

Diagnosis: Shell medium size, broadly biconic, narrowed anteriorly; spire tall; shoulders angulate or carinate; lip thickened, denticulate; external varix present; weak siphonal notch present; broad posterior notch present; columella with 4 plications, plus a weak 5th, occupying more than half the aperture.

Fossil Record: Eocene of Australia.

Nomenclature, Synonymy: This genus was placed as a subgenus of *Marginella* by Coan (1965:189). The fifth plication is not present in *Marginella* s. str. and the resemblance is superficial.

Remarks: We consider this apparently monotypic genus to be ancestral to *Protoginella* based on the presence of a weak 5th columellar plication, tall spire, and weak posterior notch. Laseron (1957:287) considered this genus to be ancestral to *Carinaginella* based on the carinate shoulders. *Carinaginella* is synonymized here with *Alaginella* because we regard carinate shoulders to be convergent and not expressing a close relationship to members of *Alaginella*, which also has 4 columellar plications. Cotton (1949:218) stated that *M. regula* was related to *M. muscaroides* Tate, 1878, a species we consider to be clearly in *Austroginella* based on the distinctively shaped lip and presence of a strong siphonal notch, and thus not closely related to *Mioginella*.

Genus *Protoginella* Laseron, 1957
(figure 57)

Protoginella Laseron, 1957:285

Type species: *Marginella lavigata* Brazier, 1877, = *Marginella (Prunum) lavigata* Brazier, 1877; OD (figure 57)

Diagnosis: Shell small to medium, white, biconic or subpyriform, strongly narrowed anteriorly; spire medium height; aperture narrow; lip strongly thickened, strongly denticulate, alate posteriorly; external varix present; posterior notch present; siphonal notch absent; columella with 4 strong plications that are excavated inside aperture, plus a "false 5th"; plications occupying more than half the aperture.

Description: Shell (figure 57) small to medium in size (adult length 4.4–7.0 mm). Color white; surface smooth, glossy. Shape biconic, subpyriform, strongly narrowed anteriorly, weakly to strongly shouldered. Spire medium height. Aperture narrow throughout. Lip strongly thickened, posterior corner strongly alate, strongly denticulate, with distinct external varix. Shell without siphonal notch, but anterior end somewhat truncate; posterior notch present at posterior corner of lip. Extent of ventral callusing undetermined. Columella with 4 strong continuous plications excavated inside aperture, plus weak "false 5th" plication or parietal lira; plications occupying 4/5 aperture length. Internal whorls presumed unmodified.

External anatomy: Unknown.

Internal anatomy: Unknown.

Radula: 1 species studied. Type 5, uniserial, ribbon short, broad. Rachidian plates barely overlapping, moderately broad (0.028 mm wide), weakly arched, with 14–15 strong cusps on posterior edge. Central cusp strongest. Anterior edge of rachidian plate moderately concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 160.

Distribution and Habitat: Indo-Pacific (2 species). Recorded from 13 to 97 m.

Fossil Record: Eocene and Pliocene of Australia, to Recent.

Nomenclature, Synonymy: A syntype of the type species is figured by Kaicher (1981:#2644) and herein (figure 57). Hedley (1901:123) emended the name to *M. laevigata*, an unjustified emendation. No evidence in the original publication itself exists of "clear evidence of an inadvertent error," and incorrect transliteration is not to be considered an inadvertent error [ICZN Art. 32(c)(ii)]. Thus, there is no homonymy with *Marginella laevigata* Eichwald, 1830. The syntype of *M. baudinensis* Smith, 1899, a synonym, was figured by Kaicher (1981:#2622). Some authors have synonymized *M. valida* Watson, 1886, which is an *Alaginella* and very distinct from *P. lavigata*.

Remarks: Laseron's original concept included *M. geminata* Hedley, 1912. This was based on the presence of a denticulate lip, a character variable in *Alaginella*, in which this species is now placed. This restricted concept of *Protoginella* is based on a strong posterior notch, columellar plications appearing excavated due to callus deposits, presence of a weak "false 5th" plication, and a strongly thickened, denticulate lip.

† Genus *Nudifaba* Eames, 1952

Marginella, subg. *Nudifaba* Eames, 1952:122

Type species: *Marginella (N.) rakhiensis* Eames, 1952 †; OD (M)

Diagnosis: Shell minute, broadly obconic; spire flat; aperture narrow; lip strongly thickened, produced on posterior corner, smooth, lacking denticulation; strong external varix present; strong posterior parietal callus deposit present near posterior commissure of lip, forming weak posterior notch; siphonal notch absent; columella with 4 strong plications occupying slightly more than half the aperture.

Fossil Record: Eocene of Pakistan.

Nomenclature, Synonymy: Currently considered a monotypic genus.

Remarks: The 4 columellar plications, smooth, strongly thickened lip that is produced or alate on the posterior corner, presence of an external varix, and absence of a siphonal notch all indicate placement in the Austroginellini and an ancestral relationship to *Alaginella*. Due to the early occurrence of this group in the Eocene of Pakistan, and the presence of a strong posterior parietal callus deposit, we consider this a separate, valid genus.

Genus *Alaginella* Laseron, 1957
(figure 58)

Alaginella Laseron, 1957:286
Carinaginella Laseron, 1957:286 [TS: *Marginella carinata* E. A. Smith, 1891; OD (M)]
† *Cassoginella* Laseron, 1957:287 [TS: *Marginella palla* Cotton, 1949 †; OD (M)]
Triginella Laseron, 1957:280–281 [TS: *Marginella malina* Hedley, 1915; OD (M)]

Type species: *Marginella ochracea* Angas, 1871; OD (figure 58)

Diagnosis: Shell minute to medium, white, biconic, obovate, or subpyriform, usually strongly narrowed anteriorly; spire low to medium height; aperture narrow to moderately narrow; lip moderately thickened, denticulate to smooth, alate posteriorly; external varix present; posterior notch weak or absent; siphonal notch absent; columella with 4 strong unexcavated plications occupying slightly more than half the aperture, lacking "false 5th" plication. Type 2 animal; siphon long; mantle papillose, extending over external shell surface.

Description: Shell (figure 58) minute to medium in size (adult length 1.7–13.0 mm). Color white; surface smooth, glossy. Shape biconic, obovate to subpyriform, usually strongly narrowed anteriorly; weakly to strongly shouldered, rarely strongly carinate. Spire usually medium height, rarely very low to low. Aperture narrow to moderately narrow, rarely broad, narrowest medially in some species. Lip moderately thickened, thickest medially to posteromedially, posterior corner strongly alate, denticulate to smooth, with a distinct external varix. Shell without siphonal notch, posterior notch weak, poorly defined to absent. Shell without obvious ventral callusing. Columella with 4 strong continuous plications occupying slightly more than half the aperture length. Internal whorls unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle covering most or all of external shell surface, papillose with conspicuous, branched papillae; foot nearly as wide as shell, twice as long; animal white, dotted with brown. [Based on description of *A. geminata* (Hedley, 1912) in Cotton (1944: 16) (as *weedingi* Cotton, 1944) plus description of *A. ochracea* (Angas, 1871), ex. unpublished mss., ex. R. Burn and D. R. Hewish].

Internal anatomy: Unknown.

Radula: 9 species studied. Type 5, uniserial, ribbon short, broad, of 20–55 plates. Rachidian plates usually overlapping, moderately broad (0.019–0.040 mm wide), weakly arched, with 11–20 strong cusps on posterior edge. The central cusp usually strongest. Anterior edge of rachidian plate slightly to strongly concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 86–174. Radular Index = 1.5–4.4.

Distribution and Habitat: S. Australian (8 species), Indo-Pacific (8 species), South African (9 species). Intertidal to 1,650 m.

Fossil Record: Miocene and Pliocene of Australia, to Recent.

Nomenclature, Synonymy: The types of *M. ochracea*, type species of *Alaginella*, and *M. carinata*, type species of *Carinaginella*, were figured by Kaicher (1981:#2618, #2682). The radulae of these two species, plus *M. malina*, type species of *Triginella*, have been studied (pers. obs. of SEMs, ex. Dean Hewish), and all three species are here considered to be congeneric. Conchological differences are considered to be of specific value only, including the carinate shoulders of *A. carinata*. *M. palla*, the type species of *Cassoginella*, has an axially costate shell. As in other austroginelline genera, this is considered to be of specific value only. The alate posterior end of lip and lack of a siphonal notch place this species in *Alaginella*. The principle of first reviser (ICZN Art. 24) is herein employed in choosing *Alaginella* over the other, more restricted names.

Remarks: The alate, flared shoulder of the aperture and the anteriorly strongly narrowed shell, combined with the lack of a strong posterior notch and lack of a "false 5th" columellar plication will serve to distinguish this group. The presence or absence of labial denticulation and axial costae are considered to be of specific difference only. The branched mantle papillae may ultimately prove to be a diagnostic character of this genus. The report on the radula in the original description of *Triginella malinoides* Gabriel, 1962, fig. 4 is apparently erroneous. We have examined SEMs of a radula (ex. Dean Hewish) from a shell intermediate between *A. malina* (Hedley, 1915) and *T. malinoides* and it is a typical *Alaginella* radula. In fact, we consider these two species synonymous. The radula figured by Gabriel is clearly not a marginellid radula and is obviously in error.

† Genus *Hiwia* Marwick, 1931

Marginella, subg. *Hiwia* Marwick, 1931:129

Type species: *Marginella (Hiwia) amplificata* Marwick, 1931 †; OD (M)

Diagnosis: Shell small, broadly biconic, strongly narrowed anteriorly; spire medium height; strong axial costae present; shoulders angulate to carinate; aperture narrow; lip thickened, smooth, not denticulate; posterior corner of lip sharply angulate; external varix present; siphonal notch absent; columella with 4 plications occupying more than half the aperture.

Fossil Record: Eocene of Australia, to Oligocene of New Zealand.

Nomenclature, Synonymy: This group was considered to be a valid genus by Coan (1965:189).

Remarks: The two included species (type species and *M. aldingae* Tate, 1878) appear to be closely related, but otherwise form a distinct, valid genus, apparently extinct since the Oligocene. A relationship to the "*Austroginella* Group" and especially *Austroginella* is indicated by the 4 columellar plications occupying more than half the aperture, but this group lacks a siphonal notch and has a narrow aperture.

Genus *Austroginella* Laseron, 1957
(figures 25, 59, 80)

Austroginella Laseron, 1957:285
Plicaginella Laseron, 1957:285 [TS: *Marginella formicula* Lamarck, 1822; OD]

Type species: *Marginella muscaria* Lamarck, 1822; OD (figure 59)

Diagnosis: Shell medium to moderately large, white, yellowish-white, or pale yellowish-orange, biconic, obovate, or subpyriform, usually strongly narrowed anteriorly; spire low to medium height with shouldered whorls; aperture broad, lip smooth, rapidly thickening posteriorly with sharply defined posterior notch; external varix

present; siphonal notch present; heavy ventral callusing usually present; columella with 4 strong plications occupying more than half the aperture. Type 2 animal; siphon long to very long; mantle smooth or weakly pustulose, extending over external shell surface.

Description: Shell (figure 59) medium to moderately large (adult length 6.2–16.3 mm). Color white, yellowish-white, or pale yellowish-orange; surface smooth, glossy, some species with weak to distinct axial costae. Shape biconic, narrowly to broadly obovate, or subpyriform, usually strongly narrowed anteriorly; weakly to strongly shouldered. Spire low to medium height; spire whorls convex or shouldered, giving uneven profile. Aperture broad, especially anteriorly. Lip moderately to strongly thickened, narrow anteriorly, rapidly thickening posteriorly but slightly narrowed at posterior fourth, smooth, lacking labial denticulation, with distinct external varix. Shell with distinct siphonal notch, and strong, grooved posterior notch at the junction of body whorl and posterior commissure of lip. Shell usually with heavy ventral callusing. Columella with 4 strong continuous plications occupying slightly more than half the aperture length. Internal whorls unmodified.

External anatomy: 4 species studied. Type 2 animal; tentacles long, slender; siphon long to very long; mantle smooth or weakly pustulose, covering most or all of external shell surface; foot very broad, 2–3 X as wide as shell, about 2 X as long; animal spotted or blotched with white, dark brown, orange, yellow, red, or green. See summary in Ponder and Taylor (1992).

Internal anatomy (figure 80): 2 species studied. Same as for "*Austroginella* Group."

Radula (figure 25): 5 species studied. Type 5, uniserial, ribbon short, broad, of 29–61 plates. Rachidian plates overlapping, moderately broad (0.029–0.114 mm wide), weakly arched, with 13–20 strong cusps on posterior edge. Central cusp strongest. Anterior edge of rachidian plate slightly to moderately concave, resulting in chevron-shaped plates. Shell length: radular width ratio = 118–162. Radular Index = 1.7–3.5.

Distribution and Habitat: S. Australian (6 species). Intertidal to 27 m.

Fossil Record: Miocene to Pleistocene of Australia, to Recent.

Nomenclature, Synonymy: The nomenclature of these two genus-group names and their type species were discussed in Coovert (1988b), in which the presence of axial costae are considered to be of specific value only.

Remarks: This well-characterized group is distinguished by the presence of 4 strong columellar plications occupying more than half the aperture, combined with the presence of a siphonal and a posterior notch, along with the distinctive lip shape. For an account of predatory shell drilling and anatomy, see Ponder and Taylor (1992).

Genus *Mesoginella* Laseron, 1957
(figure 60)

Mesoginella Laseron, 1957:282
Deviginella Laseron, 1957:283–284 [TS: *Marginella brachia* Watson, 1886, = *Marginella (Glabella) brachia* Watson, 1886; OD]
† *Hianoginella* Laseron, 1957:288 [TS: *Marginella physa* Cotton, 1949 †; OD (M)]
Sinuginella Laseron, 1957:282 [TS: *Marginella inconspicua* G. B. Sowerby II, 1846; OD]
Spiroginella Laseron, 1957:283 [TS: *Marginella leia* Cotton, 1944, = *M. turbinata* G. B. Sowerby II, 1846; OD (M)]
† *Urniginella* Laseron, 1957:287 [TS: *Marginella cassidiformis* Tate, 1878 †; OD (M)]

Type species: *Marginella turbinata* G. B. Sowerby II, 1846; OD (M) (figure 60)

Diagnosis: Shell small to medium, white or yellowish-white, rarely brownish-orange or with pale bands, biconic, obconic, obovate, or broadly cylindrical, not strongly narrowed anteriorly; spire low to medium height with evenly contoured whorls; aperture moderately narrow; lip smooth to denticulate, moderately to strongly thickened, thickest medially; external varix present; weak siphonal notch usually present; posterior notch weak to absent; ventral callusing usually absent; columella with 4 strong plications occupying slightly less to slightly more than half the aperture, 4th plication often remote. Type 2 animal; siphon long; mantle smooth or weakly pustulose, extending over external shell surface.

Description: Shell (figure 60) small to medium in size (adult length 2.5–11.0 mm). Color usually white to yellowish-white, semi-opaque to translucent, rarely brownish-orange or with pale yellow bands; surface smooth, glossy, some species with weak to distinct axial costae. Shape narrowly to broadly obovate, obconic, biconic, or broadly cylindrical, not strongly narrowed anteriorly; weakly to strongly shouldered. Spire low to medium height with evenly contoured whorls. Aperture moderately narrow, usually wider anteriorly. Lip moderately to strongly thickened, thickest medially, usually smooth, some species with weak to moderately strong labial denticulation, with distinct external varix. Siphonal notch nearly absent to weak, rarely strong, distinct or completely absent. Posterior notch weak, poorly defined or absent. Shell usually without evident ventral callusing. Columella with 4 strong continuous plications, 4th often remote, rarely with parietal tubercle appearing as "false 5th" plication. Plications occupying slightly less to slightly more than half the aperture length. Internal whorls unmodified.

External anatomy: 5 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth or weakly pustulose, asymmetrically extending over external shell surface; foot narrow to broad, slightly narrower to 1½ X as wide as shell, about 1½ X as long; animal variously spotted, blotched, or with lines of various colors,

including white, yellow, orange, brown, and black. See summary in Coovert (1987g).

Internal anatomy: 1 species studied. Same as for "*Austroginella* Group."

Radula: 16 species studied. Type 5, uniserial, ribbon short, broad, of 19–75 plates. Rachidian plates usually overlapping, moderately broad (0.018–0.050 mm wide), weakly arched, with 9–22 strong cusps along posterior edge. The central cusp (or two subcentrals) is the strongest. Anterior edge of rachidian plate slightly to strongly concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 101–221. Radular Index = 1.5–7.1.

Distribution and Habitat: Neozelanic (13 species), S. Australian (13 species), Indo-Pacific (7 species). Intertidal to 640 m.

Fossil Record: Miocene, Pliocene, and Pleistocene of Australia, to Recent.

Nomenclature, Synonymy: The nomenclature of *Mesoginella* and *Sinuginella* and their type species were discussed by Coovert (1988b). The type of *M. inconspicua* was figured by Kaicher (1981:#2702). *M. brachia*, type species of *Deviginella*, falls well within the limits of *Mesoginella*. The principle of first reviser (ICZN Art. 24) is here employed in choosing the better known *Mesoginella* over *Deviginella*. The holotype of *M. leia* was figured in Hewish and Gowlett-Holmes (1991:64, figs. E-F) and synonymized with *M. turbinata*, thus placing *Spiroginella* in synonymy. The two fossil genera *Hianoginella* and *Urniginella* are here synonymized, based on conchological characters falling within the limits of *Mesoginella*. Laseron (1957:284) used several *nomina nuda* that are apparently manuscript names for genera synonymized here. These should not be further considered.

Remarks: The presence or absence of axial costae are not considered to be a genus-level character in this group. The 4th columellar plication is often remote, i.e. separated farther from the other 3 plications. This is a rather diverse genus but all species possess the same type of radula and conchological characters.

Genus *Closia* Gray, 1857
(figure 61)

Closia Gray, 1857:36

Type species: *Closia sarda* (Kiener, 1834), = *Marginella sarda* Kiener, 1834; M (figure 61)

Diagnosis: Shell medium to moderately large, white or colored, obovate; spire immersed; lip thickened, denticulate; external varix present; siphonal notch and posterior notch absent; columella with 4 thin, sharp plications crowded anteriorly.

Description: Shell (figure 61) medium to moderately large (adult length 9.9–48.0 mm). Color grayish-white, without other markings; pale rose, pink, or orangish-yellow, with lip and apical spot darker brownish-rose or yellowish-orange; or pale yellowish- to light orange with paler mid-body band and lip darker with tiny white specks. Shell surface smooth, glossy. Shape obovate, weakly to strongly narrowed anteriorly, with rounded to angulate shoulders. Spire immersed. Aperture moderately narrow, wider anteriorly. Lip moderately to strongly thickened, strongly to very strongly denticulate in adults, with a distinct external varix. Shell without siphonal notch or posterior notch. Shell usually with evident ventral callus deposits anteriorly and especially posteriorly. Some with heavy parietal callus wash abruptly ending at entrance to aperture, creating appearance of collabral parietal callus ridge. Columella with 4 thin, sharp, continuous plications, crowded anteriorly, occupying slightly less than ⅓ to ¼ aperture length. Internal whorls presumed unmodified.

External anatomy: 1 species studied. Animal white, semi-transparent. [From description of *C. limpida* Bozzetti, 1992:11, = *C. majuscula* (Martens, 1880)]. Presumed Type 2 animal.

Internal anatomy: Unknown.

Radula: Unknown.

Distribution and Habitat: Indo-Pacific (3 species), restricted to western Indian Ocean. Recorded from 20 to 140 m.

Fossil Record: Known only from the Recent.

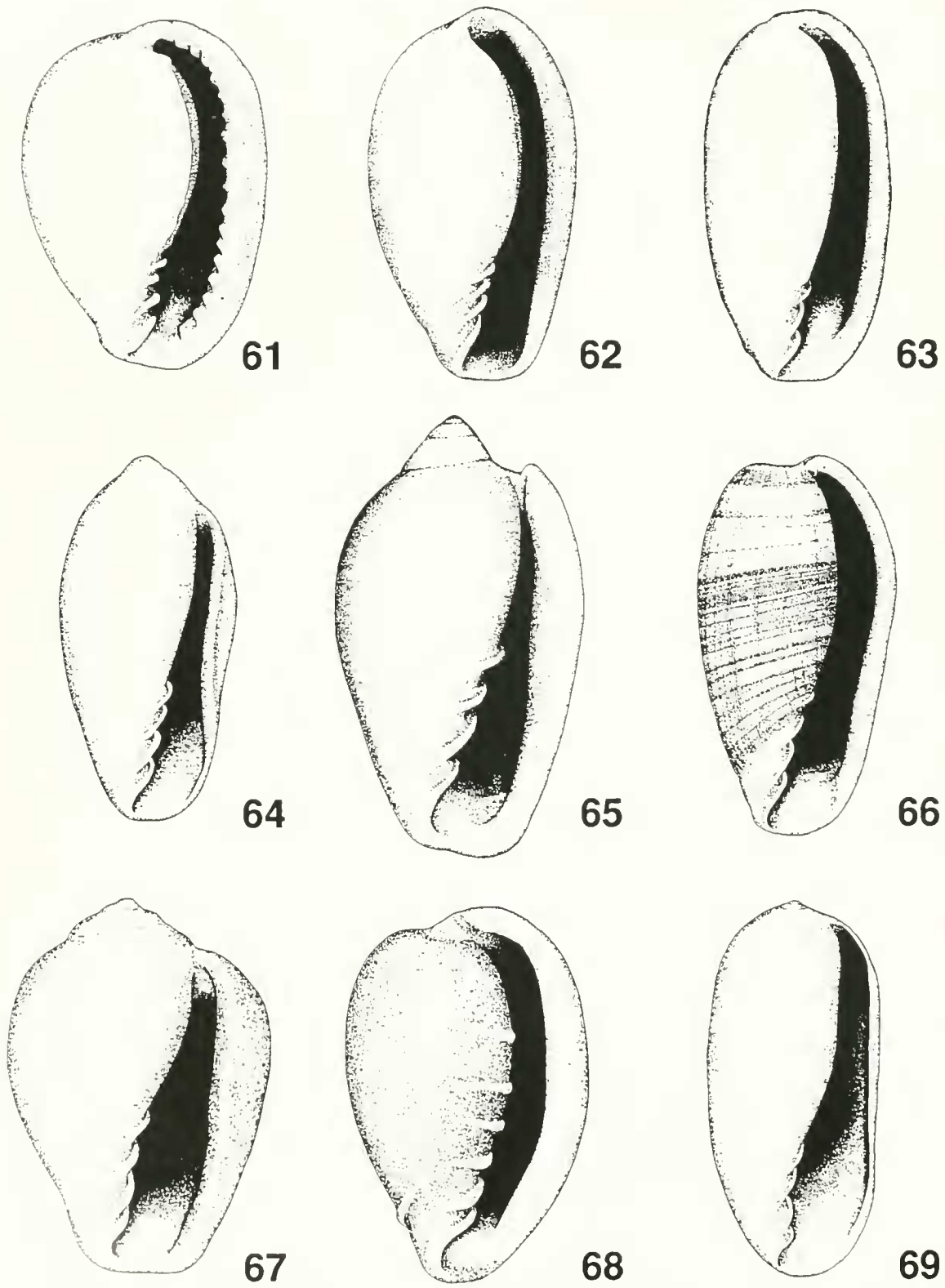
Nomenclature, Synonymy: Coan (1965:189), followed by others, considered this group to be a subgenus of *Bullata*, apparently based on the similarity to *B. lilacina* (G. B. Sowerby II, 1846). *Bullata*, which is included in Prunini based on its radula, anatomy, and fossil ancestry, has a tendency toward heavy ventral callusing and stronger columellar plications that are not nearly as crowded anteriorly as in *Closia*. Although the radula and animal are unknown, we feel that *Closia* is not closely related to *Bullata* and has a different ancestry.

Remarks: *Closia* has been variously associated with *Bullata* and *Ovaginella*. Conchologically, it comes closest to *Ovaginella*, with which it shares shell shape, and thin, sharp, anteriorly crowded columellar plications. The coarser labial denticulation, distinct shell pigmentation, heavier posteroventral callus deposit, and Indian Ocean distribution serve to distinguish it. Until the radula and animal are known, these two groups are provisionally considered distinct.

Genus *Ovaginella* Laseron, 1957
(figure 62)

Ovaginella Laseron, 1957:280

Type species: *Marginella ovulum* G. B. Sowerby II, 1846; OD (figure 62)



Figures 61–69. Shells of type species of marginellid genera, ventral views. **61.** *Closia sarda* (Kiener, 1834). GAC M1341, off Ambanja, N.E. Madagascar, dredged. Length 17.6 mm. **62.** *Ovaginella ovulum* (G. B. Sowerby II, 1846). Type, BM(NH) 80.9.8.5, locality unknown. After photograph in Kaicher (1981:#2647). Length ca. 9 mm. **63.** *Balanetta baylei* Jousseaume, 1875. GAC M1607, Margaret River, Western Australia, on beach. Length 10.5 mm. **64.** *Volvarina mitrella* (Risso, 1826). GAC M2533, Salina Bay, Malta, dredged on sandy bottom at 6 m. Length 9.3 mm. **65.** *Prunum prunum* (Gmelin, 1791). GAC M1393, Venezuela. Length 26.9 mm. **66.** *Bullata bullata* (Born, 1778). GAC M1787, Praia de Forte Gragoata, Niterói, Rio de Janeiro, Brazil. Length

Diagnosis: Shell small to medium, white, elliptic to obovate; spire immersed; lip thickened, usually smooth, rarely denticulate; external varix present; siphonal notch and posterior notch absent; columella with 4 anteriorly crowded plications.

Description: Shell (figure 62) small to medium in size (adult length 4.2–10.1 mm). Color translucent to semi-opaque white; surface smooth, glossy. Shape narrowly to broadly elliptic to obovate, weakly to strongly shouldered. Spire immersed. Aperture moderately narrow, slightly wider anteriorly. Lip moderately thickened, usually smooth, rarely weakly denticulate, with distinct external varix. Siphonal notch weak or absent; posterior notch absent. Shell usually without evident ventral callusing. Columella with 4 continuous plications crowded anteriorly, occupying distinctly less than half aperture length. Internal whorls unmodified.

External anatomy: Unknown.

Internal anatomy: Unknown.

Radula: 2 species studied. Type 5, uniserial, ribbon short, broad, of 20–31 plates. Rachidian plates overlapping, moderately broad (0.025–0.035 mm wide), weakly arched, with 8–14 strong cusps along posterior edge. The central cusp is the strongest. Anterior edge of rachidian plate slightly concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 170–285. Radular Index = 1.8–3.5.

Distribution and Habitat: Neozelanic (2 species), S. Australian (2 species). Recorded from 3 to 370 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: The type species of *Ovaginella*, *M. ovulum*, is figured by Kaicher (1981:#2674) and herein (figure 62). Coan (1965:189) placed *Ovaginella* as a subgenus of *Balanetta*, but the latter has only 3 columellar plications and a narrower shape.

Remarks: Although *Balanetta* and *Ovaginella* both have a Type 5 radula, they are considered distinct based on conchological differences.

Genus *Balanetta* Jousseaume, 1875
(figure 63)

Balanctta Jousseaume, 1875 168, 269

Type species: *B. baylei* Jousseaume, 1875; M (figure 63)

Diagnosis: Shell minute to medium, white, cylindrical to narrowly obovate; spire immersed; lip thickened, smooth; external varix present; with weak or absent siphonal notch; posterior notch absent; columella with 2 or 3 plications crowded anteriorly.

Description: Shell (figure 63) minute to medium in size (adult length 1.5–12.0 mm). Color translucent to opaque white or yellowish-white; surface smooth, glossy. Shape cylindrical to narrowly obovate, weakly to strongly shouldered. Spire immersed. Aperture moderately narrow, distinctly wider anteriorly. Lip moderately thickened, smooth, not denticulate, with a distinct external varix. Siphonal notch weak or absent, posterior notch absent. Shell without evident ventral callusing. Columella with 3 continuous plications (one species with 2), crowded anteriorly, occupying less than ¼ aperture length. Internal whorls presumed unmodified.

External anatomy: Unknown.

Internal anatomy: Unknown.

Radula: 1 species studied. Type 5, uniserial, ribbon relatively short, broad, of 29–37 plates. Rachidian plates overlapping, moderately broad (0.027–0.031 mm wide), weakly arched, with 9–14 strong cusps on posterior edge. Central cusp strongest. Anterior edge of rachidian plate slightly concave, resulting in rectangular to chevron-shaped plates. Shell length: radular width ratio = 185–239. Radular Index = 2.6–3.1.

Distribution and Habitat: S. Australian (3 species), Indo-Pacific (1 species). Intertidal to 183 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: The type species was dedicated to M. Bayle in the original description by Jousseaume (1875:269, 274) but spelled "*baylii*" in the text and "*baylei*" in the figure caption (op. cit., pl. 8, fig. 5). This is to be considered a case of multiple original spellings, which is dealt with in the ICZN [Art. 32(b)(i)]. This section, then, is subject to Section 32(c)(ii), which considers an incorrect original spelling one in which the original publication itself shows clear evidence of an inadvertent error. Because Jousseaume intended the species to be dedicated to M. Bayle, it is clear that the spelling "*baylei*" is the correct one. Tomlin (1917:252) considered "*baylei*" an error.

Remarks: The immersed spire, lack of labial denticulation, and presence of an external varix and only 3 columellar plications, distinguishes this group.

Tribe PRUNINI Coovert and Coovert, new tribe

Diagnosis: Shell small to very large, white, uniformly colored, patterned, or banded; spire immersed, or low to tall; lip thickened, smooth to denticulate; external varix present or absent; siphonal notch usually absent; posterior notch absent; columella with 2–6 plications occupying half or less of the aperture. Type 2 animal; siphon long

←

57.6 mm. **67.** *Rivomarginella morrisoni* Brandt, 1968. GAC Acc. # 11–89, Prachin River, Kabinburi, Thailand. Length 10.0 mm. **68.** *Cryptospira tricincta* (Hinds, 1844). GAC M1253, Formosa Strait, S.W. Taiwan, dredged at 37 m. Length 23.8 mm. **69.** *Hyalina pallida* (Linné, 1758). GAC M2068, St. Croix, U.S. Virgin Islands. Length 14.3 mm.

to very long; mantle smooth, pustulose, rarely distinctly papillose, usually extending over external shell surface. Type 6 radula or non-radulate. Marginellid buccal pouch present, absent in non-radulate species; odontophoral cartilages present in radulate species, fused anteriorly or both anteriorly and posteriorly; valve of Leiblein absent; esophageal caecum present; gland of Leiblein with long, convoluted duct and a terminal bulb, passing through nerve ring and emptying into anterior end of proboscis; paired salivary glands ascinous or tubular, either contained within proboscis or free, ducts either attached to walls of esophagus or free; single accessory salivary gland present or absent, ascinous or tubular.

Genus *Volvarina* Hinds, 1844
(figures 38, 64)

Marginella, section *Volvarina* Hinds, 1844:75

Type species: *Marginella nitida* Hinds, 1844, = *Marginella (Volvarina) nitida* Hinds, 1844, = *Voluta mitrella* Risso, 1826; SD Redfield, 1870:221 (figure 64)

Diagnosis: Shell small to moderately large, color translucent white, amber, or brown, usually with darker bands; spire immersed, or low to tall; lip thickened, smooth, not denticulate; external varix usually absent, but weak to strong in some species; siphonal notch absent or weak; columella with 3 or 4 plications, some species with weaker 5th or 6th, combined occupying half or less of the aperture. Type 2 animal; siphon long to very long; mantle smooth or usually pustulose, rarely distinctly papillose, usually extending over external shell surface. Type 6 radula.

Description: Shell (figure 64) small to moderately large (adult length 2.6–22.4 mm). Color translucent to opaque white, amber, or brown, usually with yellow, orange, brown, or reddish spiral bands, rarely axially streaked; surface smooth, glossy. Shape elongate to moderately broadly cylindrical, elliptic, narrowly to broadly obovate, or oblong, rarely elliptic-cylindrical with immersed spire; weakly to strongly shouldered. Spire rarely immersed, usually low, medium, or tall. Aperture narrow to moderately broad, rarely broader, usually wider anteriorly. Lip narrowly to strongly thickened, smooth, not denticulate, usually lacking an external varix, some species with weak to strong external varix. Siphonal notch rarely weak, usually absent; posterior notch absent. Ventral callusing usually not evident, present in one species group. Columella usually with 4 continuous plications; rarely with 3 plications and "false 4th" plication that joins short collabral parietal callus ridge; or 5 plications, the 5th not continuous past ½ whorl internally, plus often "false 6th" plication or parietal lira posteriorly. Plications usually occupying less than half, but some species up to half the aperture length. Internal whorls unmodified.

External anatomy: 26 species studied. Type 2 animal; tentacles long, slender; siphon long to very long; mantle smooth or usually pustulose, rarely distinctly papillose, extending over external shell surface, often nearly completely covering shell; foot moderately broad, about 1½ X shell width, 1½–2 X length; animal variously spotted or mottled in white, black, or various colors.

Internal anatomy (figure 38): 2 species studied. As in tribe. Marginellid buccal pouch present; odontophoral cartilages fused both anteriorly and posteriorly; paired salivary glands ascinous, either contained within proboscis or free, ducts either attached to walls of esophagus or free; single accessory salivary gland present, ascinous or tubular.

Radula: 43 species studied. Type 6, uniserial, ribbon short, broad, of 31–75 plates. Rachidian plates overlapping, broad (0.034–0.562 mm wide), nearly flat, with 10–33 (exceptionally 5) sharp cusps on posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 25–96. Radular Index = 1.0–4.5.

Distribution and Habitat: Neozelanic (1 species), S. Australian (2 species), Indo-Pacific (33 species), E. Pacific (3 species), W. Atlantic (24 species), Arctic (1 species), Magellanic / Antarctic (3 species), Mediterranean (1 species), W. African (29 species), South African (10 species). Intertidal to 1,780 m.

Fossil Record: Eocene of France, Oligocene to Pleistocene of W. Atlantic, early Miocene of W. Pacific, Miocene to Pliocene of Italy, Pleistocene of California, to Recent.

Nomenclature, Synonymy: As discussed in Gofas (1989b: 160), the correct type species designation, by subsequent designation, is Redfield (1870:221). Mention in Hinds (1844:75) of *M. avena* as a "typical species" does not constitute a type designation, and the Cossmann (1899: 92) designation was preceded by that of Redfield.

Remarks: Apparently the smooth mantle does not readily cover the external shell surface in the narrow, non-varicose species. The broader, varicose West African and Mediterranean species all have a pustulose mantle that more readily covers the external shell surface (see Gofas, 1989b, and Gofas & Fernandes, 1992). Several undescribed Caribbean species, discussed in Coovert and Coovert (1990) (as *Prunum* sp., red-papillose mantle; and *Volvarina* sp. SW), have a distinctly papillose mantle that readily covers the shell. This is the most widely distributed genus as currently conceived, being found in all marine provinces. See *Prunum* for further discussion.

Genus *Prunum* Herrmannsen, 1852
(figures 1, 7–8, 17–20, 27, 31, 39–42, 65)

Prunum Herrmannsen, 1852:113

† *Volutella*, subg. *Microspira* Conrad, 1868:66 [TS: *P. (sic.) oviformis* Conrad, 1868, = *Volutella (M.) oviformis* Conrad, 1868 †; M]

Egouena Jousseaume, 1875:167, 192 [TS: *E. egouen* Jousseaume, 1875, = *Marginella amygdala* Kiener, 1841; T]

† *Porcellanella* Tryon, 1882:16, (*non* White in MacGillivray, 1852) [TS: *P. bella* Conrad, 1868, = *Prunum bella* Conrad, 1868 †; OD (M)] [publ. as *nomen nudum* in Conrad, 1863: 564, TS: *P. bella* Conrad, 1863, *nomen nudum*; M]

Marginella, subg. *Volvarina*, section *Leptegouana* Woodring, 1928:237–238 [TS: *Voluta guttata* Dillwyn, 1817; OD]

Type species: *Voluta prunum* Gmelin, 1791; M (figure 65)

Diagnosis: Shell small to large, usually thick, opaque, white or uniformly colored, often patterned, but usually not simply with dark, narrow bands; shell variously shaped; lip moderately to strongly thickened, smooth to denticulate; external varix usually present; siphonal notch usually absent; posterior notch absent; shell usually with heavy ventral callusing; columella with 4 plications occupying half or less of the aperture. Type 2 animal; siphon long to very long; mantle smooth, extending over external shell surface. Type 6 radula.

Description: Shell (figures 1, 65) small to large (adult length 3.3–44.1 mm). Shell usually thick, opaque, rarely translucent, white or colored tan, gray, brownish-gray, orange, or pink; uniformly colored, streaked, or spotted, or with paler spiral bands on colored species, some species with opaque white flecks overlaying other patterns, rarely banded with darker color. Surface smooth, glossy. Shape obovate, oblong, subtriangular, biconic, or rarely subcylindrical; weakly to strongly shouldered. Spire rarely immersed, usually low to medium height. Aperture narrow to moderately broad, wider anteriorly. Lip moderately to very strongly thickened, in one group much thinner anteriorly, smooth, often weakly to distinctly denticulate; usually with very distinct, rarely duplicate, external varix that is weak to absent in some species. Siphonal notch usually absent, rarely weakly developed; posterior notch absent. Ventral callus usually heavy, often with strongly produced deposit near posterior commissure of lip. Columella usually with 4 continuous plications, rarely with weak 5th plication. Plications usually occupying half or less of aperture length. Internal whorls unmodified.

External anatomy (figures 7, 8): 17 species studied. Type 2 animal; tentacles long, slender; siphon long to very long; mantle smooth, symmetrically extending over external shell surface, often nearly completely covering shell; foot broad and long, about 1½ X shell width, 2 X shell length; animal variously marked with tiny dots, spots, blotches, or lines of various colors.

Internal anatomy (figures 31, 39–42): 6 species studied. As in tribe. Marginellid buccal pouch present; odontophoral cartilages fused anteriorly or both anteriorly and posteriorly; paired salivary glands ascinous or tubular, free, ducts either attached to walls of esophagus or free; single tubular accessory salivary gland present or absent.

Radula (figures 17–20, 27): 22 species studied. Type 6, uniserial, ribbon short, broad, of 24–59 plates. Rachidian plates overlapping, broad (0.096–0.920 mm wide), nearly flat, with 16–45 sharp cusps on posterior edge. Anterior edge of rachidian plate generally straight, producing elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 30–103. Radular Index = 0.6–2.9.

Distribution and Habitat: Indo-Pacific (2 species), E. Pacific (7 species), W. Atlantic (52 species), W. African (3 species). Intertidal to 1,840 m.

Fossil Record: Eocene of Mississippi, Oligocene to Pleistocene of W. Atlantic, to Recent.

Nomenclature, Synonymy: The four genus-group names synonymized under *Prunum* differ mainly in degree of callusing, spire development, and degree of thickening and denticulation of the outer lip, all considered to be of specific value only. *Egouena* is in the same species group as *P. prunum* based on its type species *E. egouen*, a junior synonym of *M. amygdala*. This is supported by our observations of specimens of *P. marginatum* (Born, 1778), in which subadults are extremely similar to *P. prunum*, whereas fully adult specimens with heavy callus deposits are obviously close to *P. amygdalum*. All share the same brown apertural coloration and combined with several other species form a closely related species group. The 3 multiple original spellings of *Egouena* were listed and discussed in Coan (1965:189), where Neave (1939: 2:199) was listed as the first revisor. The other 3 genus-group names are not quite as closely related, but certainly appear to be congeneric. The holotype of *Volutella oviformis* was figured by Gardner (1937:pl. 47, figs. 11–12). The type of *P. bellum* was figured by Olsson and Harbison (1953:pl. 30, fig. 4). Coan (1965:189) synonymized *Egouena*, *Porcellanella*, and *Leptegouana* under *Prunum*. Roth (1978:8) tentatively considered *Egouena* and *Leptegouana* synonyms of *Microspira*. Some of these genus-group names could be employed as subgeneric groups after all *Prunum* and *Volvarina* are fully revised, but this would probably necessitate introducing additional formal names. We feel that recognition of informal species groups would be a better solution. Much research remains to be done along these lines, especially with the anatomy and fossil fauna.

Remarks: The concept of this genus outlined in Coovert (1988c) has been further modified, partially based on the work of Gofas (1989b) and Gofas and Fernandes (1992) on *Volvarina*. These authors placed the majority of West African species, formerly included in *Prunum*, in *Volvarina*. They stated that the separation of these two genera was largely subjective as far as shell features, a contention with which we agree. Species of *Prunum* have a smooth mantle, whereas the West African *Volvarina* have a pustulose or papillose mantle. The group of non-varicose, narrow *Volvarina* often have a smooth mantle, but in at least one species group ("*rubella* group," see Coovert & Coovert, 1990), their radula distinguish them from *Prunum*. Also, the ontogenetic development of the thickened outer lip in varicose and non-varicose species may further distinguish these genera (cf. section on shell

morphology). The key to genera will serve to identify these two groups based on current concepts.

A satisfactory solution to this complex situation will only be realized through a complete revision of all species groups in both genera, based on shell and anatomical features in combination with a study of the fossil record. We feel that the large group of western Atlantic species assigned to *Prunum*, both varicose and non-varicose, forms a natural assemblage distinct from the western Atlantic species assigned to *Volvarina*. Three major species radiations apparently occurred: eastern Atlantic *Volvarina* with a pustulose mantle; western Atlantic *Prunum* with a smooth mantle; and a much more widespread group of narrow, non-varicose *Volvarina*.

Genus *Bullata* Jousseaume, 1875
(figure 66)

Bullata Jousseaume, 1875:167, 250
Marginella, subg. *Volutella* Swainson, 1830:(2)1, *Marginella* pl. 1 (*non* Perry, 1810) [TS: *Marginella bullata* Lamarck, 1822, = *Voluta bullata* Born, 1778; OD]
Gibberulina Monterosato, 1884:139 [invalid emendation, as "nom. sost."]

Type species: *Bullata bullata* (Born, 1778), = *Voluta bullata* Born, 1778; T (figure 66)

Diagnosis: Shell moderately large to very large, colored and banded or patterned, elliptic to oblong or obovate; spire immersed or nearly so; lip thickened, denticulate in adults; external varix present; siphonal notch absent; columella with 4 strong plications occupying less than half the aperture but are not crowded anteriorly. Type 2 animal; siphon long; mantle extension undetermined. Type 6 radula.

Description: Shell (figure 66) moderately large to very large (adult length 16.8–90.0 mm). Color yellowish-orange to orangish- or pinkish-brown, spirally banded or with white spots, lip pink, yellow, or orange, darker than shell color. Shell surface smooth, glossy. Shape elliptic to oblong or obovate, moderately to strongly shouldered. Spire immersed or nearly so. Aperture narrow to moderately broad, wider anteriorly. Lip moderately to strongly thickened, weakly to strongly denticulate in adults, with a distinct external varix. Siphonal notch, posterior notch absent. Parietal callusing weakly to strongly developed, especially posteriorly, absent in type species. Columella with 4 continuous plications occupying less than half the aperture length. Internal whorls unmodified.

External anatomy: 1 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle extension undetermined; foot moderately broad, about 1½ X shell width, slightly longer than shell; animal marked with fine, narrow red lines on cream background. [Based on dissection of *Bullata bullata*].

Internal anatomy: 1 species studied. As in tribe. Marginellid buccal pouch present.

Radula: 1 species studied. Type 6, uniserial, ribbon short, broad, of 47 plates. Rachidian plates overlapping, broad (0.825 mm wide), nearly flat, with 40 sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 63. Radular Index = 1.2.

Distribution and Habitat: W. Atlantic (4 species). Recorded from 1 to 60 m.

Fossil Record: Miocene and Pliocene of W. Atlantic, to Recent.

Nomenclature, Synonymy: Nomenclature of *Gibberulina* was discussed in Coovert (1987h:27).

Remarks: The large, patterned shells with an immersed spire and 4 moderately heavy columellar plications not crowded anteriorly serve to distinguish this group. The presence of an esophageal caecum clearly places this genus in the Prunini. As here defined, this group is restricted to the Caribbean province, where it evolved in the Miocene as a direct offshoot of *Prunum*.

Genus *Rivomarginella* Brandt, 1968
(figure 67)

Rivomarginella Brandt, 1968:275

Type species: *R. morrisoni* Brandt, 1968; (OD) M (figure 67)

Diagnosis: Shell small to medium, translucent, lightly colored, shape obconic to subpyriform; spire medium height; aperture broad; lip thickened, smooth; external varix present; siphonal notch absent; with minutely granulated apical and ventral callusing; columella with 4 plications occupying half the aperture length. Type 2 animal; siphon long; mantle smooth, extending over external shell surface. Type 6 radula.

Description: Shell (figure 67) small to medium in size (adult length 5.4–11.3 mm). Color translucent yellowish-white to brownish-white, some species with 1 or 2 obscure spiral bands; surface smooth, glossy. Shape broadly obconic to subpyriform, moderately to strongly shouldered. Spire medium height. Aperture moderately broad to broad, wider anteriorly. Lip moderately thickened, smooth, lacking denticulation, with a distinct external varix. Siphonal notch, posterior notch absent. Shell with minutely granulated ventral and apical callusing. Columella with 4 continuous plications occupying half the aperture length. Internal whorls presumed unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth, extending almost completely over external shell surface; foot moderately broad; animal pigmented with blackish-brown, black, or yellow dots or blotches. The penis was described by Brandt (1968:277) as long, simple, and lacking appendages.

Internal anatomy: Unknown.

Radula: 2 species studied. Type 6, uniserial, ribbon short, broad, of 38–47 plates. Rachidian plates overlapping, broad, nearly flat, with 18–29 sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. No further data available.

Distribution and Habitat: Indo-Pacific (2 species), found in freshwater in S.E. Asia.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: See Brandt (1968:pl. 10, fig. 63) for a photograph of the holotype of the type species.

Remarks: Subadult shells show that the lip is first reflected, then gradually thickened by callus deposits. This is unlike *Volvarina*, which initially has the lip curved in. Thus, we consider *Rivomarginella* to be more closely allied to the *Prunum* lineage. *Eratoidea* was considered by Brandt (1968:275) to be the closest relative, but it is apparently non-radulate and has stronger columellar plications occupying more than half the aperture. For further information see Brandt (1974), Coomans and Clover (1972), and Djajasasmita and Coomans (1980).

Genus *Cryptospira* Hinds, 1844
(figure 68)

Marginella, section *Cryptospira* Hinds, 1844:76

Type species: *Marginella tricincta* Hinds, 1844, = *Marginella (Cryptospira) tricincta* Hinds, 1844; SD (M) Gray, 1847:142 (figure 68)

Diagnosis: Shell medium to large, opaque, uniformly colored or with bands or patterned; spire immersed or low; lip thickened, smooth or denticulate; external varix present; siphonal notch absent; columella with 4 to 6 plications. Type 2 animal; siphon long; mantle smooth, extending over external shell surface. Type 6 radula.

Description: Shell (figure 68) medium to large (adult length 6.2–46.0 mm). Color usually uniformly opaque gray or flesh-colored to pale brown, many with narrow spiral lines, undulating longitudinal zig-zag lines, longitudinal streaks, or spiral lines crossed by longitudinal streaks, lip often differentially colored. Often relatively thick-shelled, surface smooth, glossy. Shape cylindrical, elongate to broadly elliptic, obovate, pyriform, or subtriangular, moderately to strongly shouldered. Spire immersed or low. Aperture narrow to moderately broad, wider anteriorly. Lip moderately to strongly thickened, smooth or with weak to strong denticulation in adults, with a distinct external varix that is rarely duplicate. Siphonal notch absent or at most very weakly developed; posterior notch absent, weak notch present between posterior parietal callus deposit and posterior lip commissure. Shell often with anterior or posterior ventral parietal callusing. Columella with 4 to 6 continuous plications occupying distinctly less than half to more than half the aperture length. Internal whorls unmodified.

External anatomy: 4 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth, extending symmetrically or nearly so over external shell surface; foot moderately broad, about 1½ X shell width, 1½ X length; animal uniformly colored or brightly marked with streaks of red on yellow ground color.

Internal anatomy: Unknown.

Radula: 4 species studied. Type 6, uniserial, ribbon short, broad, of 36–50 plates. Rachidian plates overlapping, broad (0.158–0.403 mm wide), nearly fla', with 9–28 sharp cusps along posterior edge. Anterior edge of rachidian plate generally straight, resulting in elongate, rectangular "comb-like" plates. Shell length: radular width ratio = 35–77. Radular Index = 1.4–2.3.

Distribution and Habitat: Indo-Pacific (15 species). Recorded from 0.6 to 123 m.

Fossil Record: Pliocene of Java, to Recent.

Nomenclature, Synonymy: The earliest type species designation is by Gray (1847:142), as noted in Coan (1965: 189). Besides being predated by Gray, Cossmann's (1899: 94) designation of *Marginella quinqueplicata* Lamarck, 1822, as type species, is invalid because this was not an included species of Hinds. See Palmer (1937:418) for comments on nomenclature, but note that Hinds' useage of division places this taxon as a genus-group name (ICZN, Art. 10e). We do not consider *Euryentome* to be closely related to *Cryptospira*. Coan (1965:189) placed *Cryptospira* as a subgenus of *Bullata*. We consider these two groups to have separate origins, *Bullata* being a direct descendant of Caribbean *Prunum*, whereas *Cryptospira* is restricted to the western Indo-Pacific where it evolved.

Remarks: See Coomans (1969) for further information. The large, thick, colored, frequently patterned shells, often with 5 or 6 columellar plications, serve to differentiate this group. One species group within the genus has distinctively gray-colored shells. As defined and restricted geographically, this genus forms a compact, closely related group.

Genus *Hyalina* Schumacher, 1817
(figures 32, 69)

Hyalina Schumacher, 1817:234
Marginella, subg. *Volvarina*, section *Neovolvaria* Fischer, 1883: 602 [TS: *Marginella pallida* (Linné, 1767), = *Bulla pallida* Linné, 1758; M]

Type species: *Hyalina pellucida* Schumacher, 1817, = *Bulla pallida* Linné, 1758; M (figure 69)

Diagnosis: Shell small to large, white to lightly colored, hyaline or translucent, thin-shelled; spire low to medium height; aperture broad; lip thin, smooth; external varix weak to absent; siphonal notch absent; ventral callusing

absent, columella with 2 to 4 plications occupying less than half the aperture. Type 2 animal; siphon long; mantle smooth. Non-radulate.

Description: Shell (figure 69) small to large (adult length 4.0–29.0 mm). Color white, hyaline or translucent, cream to amber or brown, rarely with faint yellowish-white bands or numerous spiral lines. Thin-shelled, surface smooth, glossy. Shape broadly cylindric to obovate, weakly to moderately shouldered. Spire low to medium height. Aperture moderately broad to broad, usually distinctly wider anteriorly. Lip moderately thin, smooth, lacking denticulation; external varix weak to absent. Siphonal notch, posterior notch, ventral callusing absent. Columella with 2–4 continuous plications occupying distinctly less than half the aperture length. Internal whorls unmodified.

External anatomy: 3 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth, apparently extending over external shell surface; foot moderately broad, about 1½ X shell width, 1½ X length; animal white or translucent, uniformly colored or spotted and flecked with orange and black.

Internal anatomy (figure 32): 2 species studied. As in tribe. Marginellid buccal pouch absent, paired salivary glands tubular, free, ducts free, single accessory salivary gland present, tubular.

Radula: Non-radulate, completely lacking buccal mass, including odontophore. 3 species known or strongly suspected to be non-radulate.

Distribution and Habitat: Indo-Pacific (1 species), W. Atlantic (3 species), Magellanic / Antaretic (2 species), South African (5 species). Intertidal to 1,340 m.

Fossil Record: Pliocene of Florida, to Recent.

Nomenclature, Synonymy: Coan and Roth (1976) gave a complete discussion of *Hyalina* and its type species. They designated (op. cit. fig. 1) the same specimen as neotype for both *Bulla pallida* Linné, 1758 and *Hyalina pellucida* Schumacher, 1817, placing *Neovolvaria* as an objective synonym of *Hyalina*.

Remarks: The complete lack of a radula and buccal mass at first suggested placement of this genus with the non-radulate marginellines, but conchological features did not conform. Subsequent dissection of a specimen of *H. pallida* revealed the presence of an esophageal caecum, a diagnostic feature of the Prunini. The thin, translucent shells, a weak or absent external varix, and 2, 3, or 4 columellar plications will generally serve to distinguish this genus.

Tribe MARGINELLINI Fleming, 1828:328

Diagnosis: Shell minute to very large, white, uniformly colored, or patterned, biconic, obconic, or broadly obovate; spire low to tall; lip thickened, smooth or denticulate; external varix present; siphonal notch present or absent; columella with 4 or 5 strong plications occupying half or more of the aperture. Type 2 animal; siphon long; mantle smooth or papillose, variably extending over external shell surface. Non-radulate, lacking entire buccal mass, including odontophore and cartilages. Proboscis rounded, blunt, or distally pointed; marginellid buccal pouch absent; valve of Leiblein absent; esophageal caecum absent; gland of Leiblein with a terminal bulb and a long, convoluted duct that passes through nerve ring and empties into anterior end of proboscis; paired salivary glands acinous or tubular, either contained within proboscis or free, ducts either attached to walls of esophagus or free; single accessory salivary gland present, tubular.

† Genus *Stazzania* Sacco, 1890a

Marginella, subg. *Stazzania* Sacco, 1890a:138 (245); 1890b:26 (318)

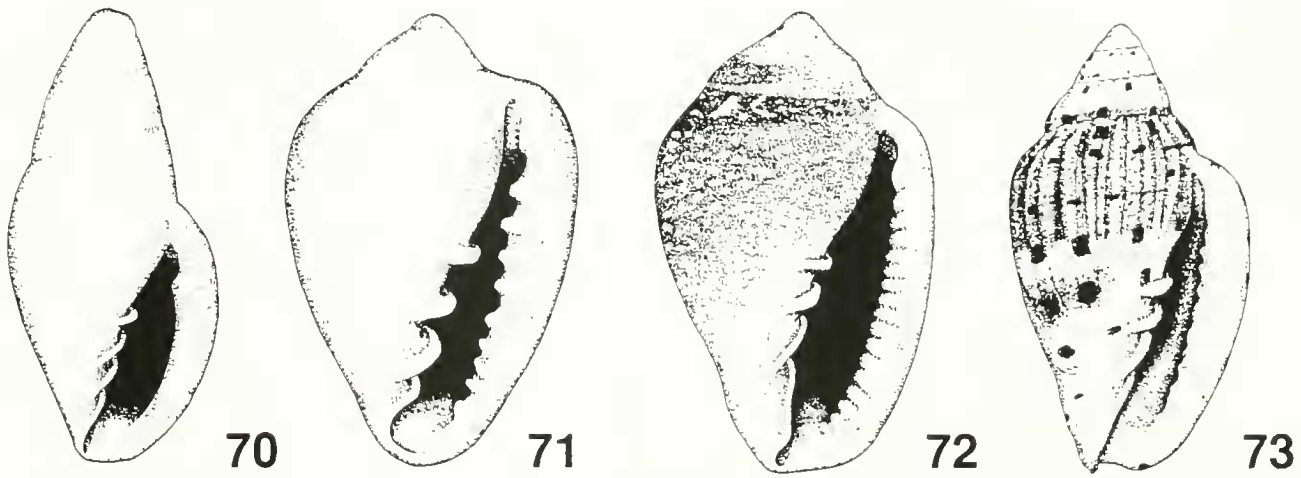
Type species: *Marginella (Stazzania) emarginata* Sismonda, 1847, = *Marginella emarginata* Sismonda, 1847 †; M

Diagnosis: Shell minute to moderately large, narrowly to broadly biconic or broadly obovate; spire medium to tall; aperture narrow; lip thickened, smooth or denticulate, often with stronger or single posterior denticle; external varix present; siphonal notch absent; columella with 4 or 5 strong plications occupying more than half the aperture; collabral parietal callus ridge present, usually connecting with bifurcated outer ends of plications.

Fossil Record: Eocene of France, to upper Miocene of Italy.

Nomenclature, Synonymy: Many European paleontologists synonymize *Dentimargo* under *Stazzania* (e.g. Gougerot & Le Renard, 1979; Nieulande, 1981; Le Renard & Nieulande, 1985), apparently based on similarities in shell shape and the presence of bifurcated columellar plications in some species of both groups. The bifurcated plications in *Stazzania* result from thin, paired callus ridges on their distal ends joining a collabral parietal callus ridge. However, in fossil species we assign to *Dentimargo*, bifurcated columellar plications are fundamentally different, being thick and broad, with a U-shaped notch distally that creates the bifurcate appearance. Species of *Dentimargo* with a collabral callus ridge do not have this ridge intersecting the distal ends of the plications. Most Recent species of *Dentimargo* have simple, unmodified plications. The type species of *Stazzania* is significantly larger than the relatively small Eocene species herein assigned to the same group, but has a very similar shape.

Remarks: *Stazzania* is here considered to be an extinct, separate lineage from the contemporaneous *Dentimargo*. *Dentimargo*, besides differing in plications, is generally narrower with a broader aperture.



Figures 70–73. Shells of type species of marginellid genera, ventral views. **70.** *Dentimargo dentifera* (Lamarck, 1803). GAC Acc. # 35–87, fossil, Lutetian of the Eocene, Paris Basin, Fercourt, France. Length 4.6 mm. **71.** *Eratoidea margarita* (Kiener, 1834). GAC M2079, Water Island, St. Thomas, Virgin Islands. Length 8.0 mm. **72.** *Marginella glabella* (Linné, 1758). GAC M1322, Cape Verde Islands. Length 38.7 mm. **73.** *Glabella faba* (Linné, 1758). GAC M1720, Dakar, Senegal, West Africa, under rocks at 15 m. Length 18.5 mm.

Genus *Dentimargo* Cossmann, 1899
(figures 33, 70)

Marginella, subg. *Marginella*, section *Dentimargo* Cossmann, 1899:90

Volvarinella Habe, 1951:101–102 [TS: *V. makiyamai* Habe, 1951; OD]

Marginella, subg. *Eburnospira* Olsson & Harbison, 1953:201–202 [TS: *Marginella eburneola* Conrad, 1834 †; OD]

Longinella Laseron, 1957:286, (*non* Gros & Lestage, 1927) [TS: *Marginella maugeana* Hedley, 1915, OD]

Type species: *Marginella dentifera* Lamarck, 1803 †; OD (figure 70)

Diagnosis: Shell small to medium, white or uniformly colored, usually banded, usually biconic; spire medium to tall; aperture moderately broad to broad; lip thickened, smooth or denticulate, often with stronger or single posterior denticle; external varix present; siphonal notch absent; columella with 4 strong plications occupying more than half the aperture. Type 2 animal; siphon long; mantle smooth or weakly papillose, extending over external shell surface.

Description: Shell (figure 70) small to medium in size (adult length 2.4–12.0 mm). Color translucent to subopaque, white, cream, to brown, usually with 1–4 narrow, yellow or brown bands. Shell surface smooth, glossy, rarely with weak to distinct axial costae. Shape narrowly to broadly biconic, rarely narrowly subovate; weakly to strongly shouldered. Spire height medium to tall, rarely stepped. Aperture moderately broad to broad, wider anteriorly. Lip thin to moderately thickened, rarely strongly thickened, smooth to denticulate, often with stronger or single denticle at posterior fourth of lip, with a distinct external varix. Siphonal notch absent, rarely very weakly indicated; posterior notch usually absent, at most weakly indicated. Ventral callusing usually absent. Columella with 4 strong continuous plications occupying more than half the aperture length. Internal whorls unmodified.

External anatomy: 7 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth or weakly papillose, extending over external shell surface, often nearly completely covering shell; foot moderately narrow to moderately broad, about 1–1½ X shell width, and 1–1½ X length; animal variously spotted or blotched with black, opaque white, or red, or with opaque white lines. Penis with sharply pointed distal or posterodistal appendage.

Internal anatomy (figure 33): 2 species studied. As in tribe. Proboscis pointed distally; paired salivary glands ascinous or tubular, contained within proboscis, ducts free.

Radula: Non-radulate, completely lacking buccal mass, including odontophore. 9 species known or strongly suspected to be non-radulate.

Distribution and Habitat: Neozelanic (10 species), S. Australian (8 species), Indo-Pacific (28 species), E. Pacific (4 species), W. Atlantic (15 species), W. African (2 species), South African (3 species). Intertidal to 1,300 m.

Fossil Record: Eocene of France, Eocene to Pleistocene of W. Atlantic, Oligocene to Pliocene of Australia, Miocene to Pliocene of W. Pacific, to Recent.

Nomenclature, Synonymy: Roth (1978:12) synonymized all of the above genus-group names, a view with which we agree. Powell (1971:223) had previously synonymized *Longinella* under *Volvarinella*. A cotype of *M. maugeana* was figured by Kaicher (1981:#2628), who

placed it in *Dentimargo*, treating *Longinella* as a subgenus. The type of *M. eburneola* was figured in Olsson and Harbison (1953:pl. 30, fig. 8). The characters separating these groups are viewed as specific differences only. The gender of *Dentimargo*, based on the Latin noun *margo* can be treated as either masculine or feminine. Because the combination "*Dentimargo dentifera*" used by Cossmann (1899:pl. 4, fig. 15) is generally considered shorthand for *Marginella (Dentimargo) dentifera*, there is no direct evidence of intended gender for *Dentimargo* by Cossmann [(ICZN Art. 30(a)(1)]. Thus, the name is to be treated as masculine.

Remarks: This is a widely distributed group, both spatially and temporally. Eventually, a thorough revision may enable species groups to be delineated. Until a thorough knowledge of the phylogeny is known, useage of informal species groups is a better solution than recognition of subgenera.

Genus *Eratoidea* Weinkauff, 1879
(figure 71)

Marginella, section *Marginella*, gruppe *Eratoidea* Weinkauff, 1879:140

Type species: *Marginella margarita* Kiener, 1834; SD Cossmann, 1899:87 (figure 71)

Diagnosis: Shell minute to medium, white or uniformly colored, rarely banded, broadly biconic; some species axially costate; spire low to medium, often stepped; lip thickened, denticulate; external varix present; siphonal notch absent; columella with 4 strong plications occupying half or more of the aperture. Type 2 animal; siphon long; mantle papillose, extending over external shell surface.

Description: Shell (figure 71) minute to medium size (adult length 1.9–11.0 mm). Color usually translucent to subopaque white, less commonly deep rose, rarely translucent white with 2 narrow brown spiral bands. Shell surface smooth, glossy, some species with weak to distinct axial costae. Shape broadly biconic, weakly to strongly shouldered. Spire low to medium height, often weakly to distinctly stepped. Aperture moderately narrow to broad, not usually distinctly wider anteriorly. Lip weakly to strongly thickened, weakly to distinctly denticulate, with a distinct external varix. Siphonal notch absent; posterior notch usually absent to at most weakly indicated. Shell without evident ventral callusing. Columella with 4 strong continuous plications occupying half to more than half the aperture length. Internal whorls unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle papillose with very long papillae in *E. hematita* (Kiener, 1834), extending almost completely over external shell surface, undetermined in *E. margarita* (Kiener, 1834); foot moderately narrow to moderately broad, about 1–1½ X shell width, 1–1½ X length; animal variously dotted or spotted with brown, yellow, or opaque white. [Based on pers. obs. of photographs ex. W. R. Liltved and R. Lipe].

Internal anatomy: Unknown.

Radula: We have attempted routine extraction of radulae from 2 specimens of *E. margarita* and found no radula. Based on this and conchological affinities with other non-radulate genera, we strongly suspect that this genus is also non-radulate.

Distribution and Habitat: W. Atlantic (9 species). Recorded from 1 to 1,470 m.

Fossil Record: Miocene of Caribbean, to Recent.

Nomenclature, Synonymy: Although Weinkauff (1879) used the single genus *Marginella*, he proposed an outline classification that included the new "gruppe" *Eratoidea*. His "section" apparently corresponds to subgenus, whereas "gruppe" corresponds to section. This genus was placed as a synonym of *Marginella (Gibberula)* by Coan (1965:189). *Gibberula* is a cystiscid genus completely unrelated to *Marginella* or *Eratoidea*.

Remarks: The 4, strong, continuous plications occupying more than half the aperture, lack of an anterior notch, and strongly denticulate lip serve to distinguish this group and to place it in Marginellini. The type species has variably low, weak axial costae, relating it to the smaller axially costate species.

† Genus *Euryentome* Cossmann, 1899

Cryptospira, subg. *Cryptospira*, section *Euryentome* Cossmann, 1899:95

Type species: *Marginella crassilabra* Conrad, 1833 (non *Marginella crassilabra* Bory de St. Vincent, 1827), = *Marginella silabra* Palmer, 1937 (nom. nov.), = *Marginella anatina* Lea, 1833 †; OD

Diagnosis: Shell medium size; lip strongly thickened, strongly denticulate on its sharp inner edge; strong external varix present; weak siphonal notch present or absent; very deep posterior notch present; columella with 4 continuous plications, often with weak 5th plication, and 4 to 5 parietal lirae in some species.

Fossil Record: Eocene of Alabama and Mississippi, to Miocene of Trinidad.

Nomenclature, Synonymy: The correct name for the type species is *M. anatina* Lea, 1833, the next available name for the junior primary homonym *M. crassilabra* Conrad, 1833. The replacement by Palmer (1937:416–417) was unnecessary and is therefore a junior synonym. Lea's type of *M. anatina* (*fide* Palmer & Brann, 1966: 618) was figured in Palmer (1937:pl. 89, fig. 10).

Remarks: The presence of parietal lirae initially caused us to consider placement in the Cystiscidae, but examination of a shell of *E. columba* (Lea, 1833) revealed

unmodified internal whorls with 4 continuous plications. The 4 strong plications, a very strong posterior notch, and probable relationship to S.E. U.S. Eocene *Dentimargo* cause us to place this genus in the Marginellini.

† Genus *Simplicoglabella* Sacco, 1890b

Marginella, subg. *Glabella*, section *Simplicoglabella* Sacco, 1890b:21 (313)

Type species: *Marginella (Glabella) taurinensis* Michelotti, 1847 †; SD (M) Eames, 1952:119

Diagnosis: Shell medium to large, narrowly to moderately broadly biconic; spire medium to tall; aperture moderately broad; lip thickened, smooth, not denticulate; external varix present; siphonal notch very weak to absent; columella with 4 strong plications occupying more than half the aperture.

Fossil Record: Miocene of Italy.

Nomenclature, Synonymy: Treated as a subgenus of *Marginella* in Coan (1965:189).

Remarks: This group is an extinct lineage related to *Marginella*, differing in its narrower shape and generally taller spire.

Genus *Marginella* Lamarck, 1799
(figures 34, 72)

Marginella Lamarck, 1799:70
† *Marginella*, subg. *Glabella*, section *Denticuloglabella* Sacco, 1890b:25 (317) [TS: *Marginella (Glabella) deshayesi* Michelotti, 1847 †; M]
Cucumis Deshayes, 1830:34 [in synonymy]
Porcellana Gray, 1847:142 (non Lamarck, 1801) [TS: *Voluta glabella* Linné, 1758; OD (M)]
Pseudomarginella Maltzan, 1880:108 [TS: *P. adansoni* Maltzan, 1880, = *Voluta glabella* Linné, 1758; M]

Type species: *Voluta glabella* Linné, 1758; M (figure 72)

Diagnosis: Shell small to very large, white to colored, always patterned, biconic to obconic, lacking axial costae; spire low to medium height; aperture broad; lip thickened, smooth to denticulate; external varix present; siphonal notch usually present; columella with 4 strong plications occupying more than half the aperture. Type 2 animal; siphon long; mantle smooth, usually not readily extending over external shell surface.

Description: Shell (figure 72) small to very large (adult length 3.5–74.1 mm). Color white, cream, tan, gray, or reddish-orange to brown, always with pattern of white to dark dots or spots, spiral lines or bands, or mottled, or with axial streaks or lines, or various combinations. Shell surface smooth, glossy. Shape biconic to obconic, rarely narrowly biconic, weakly to strongly shouldered. Spire low to medium height, rarely tall. Aperture moderately broad to broad, wider anteriorly. Lip moderately thin to strongly thickened, smooth to weakly or strongly denticulate, with a distinct external varix. Siphonal notch usually distinct, absent to weak in some species. Posterior notch absent to weak or distinct. Ventral callusing usually absent, strong parietal callus present in some species. Columella with 4 strong continuous plications occupying more than half the aperture length. Internal whorls unmodified.

External anatomy: 24 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle smooth, apparently not readily extending over external shell surface in most species; foot moderately broad, about 1½ X shell width, and 1–1½ X length; animal variously spotted, mottled, streaked, or lineated with white, black, red, or yellow on a translucent or variously colored background.

Internal anatomy (figure 34): 3 species studied. As in tribe. Proboscis rounded or blunt distally; paired salivary glands tubular, free, ducts attached to walls of esophagus.

Radula: Non-radulate, completely lacking buccal mass, including odontophore. 16 species known or strongly suspected to be non-radulate.

Distribution and Habitat: Indo-Pacific (5 species), W. Atlantic (1 species), W. African (32 species), South African (25 species). Intertidal to 2,083 m.

Fossil Record: Miocene and Pliocene of Italy, to Recent.

Nomenclature, Synonymy: The type species of *Denticuloglabella*, *M. deshayesi*, falls well within the range of *Marginella* and this genus is here synonymized. For a discussion of the "pseudogenus" *Pseudomarginella*, see Cooke (1922).

Remarks: This group is distinguished by the 4 strong plications occupying more than half the aperture, plus the colored, patterned shell and lack of axial costae. For discussion of the *M. musica–diadochus* group, see Coovert (1989a).

Genus *Glabella* Swainson, 1840
(figure 73)

Glabella Swainson, 1840:133, 324.
Marginella, section *Phaenospira* Hinds, 1844:72 [TS: *Marginella noduta* (*sic.*) Hinds, 1844, = *Marginella nodata* Hinds, 1844; SD (M) Gray, 1847:142]
Marginella, subg. *Marginella*, section *Faba* Fischer, 1883:602 [TS: *Marginella faba* (Linné, 1758), = *Voluta faba* Linné, 1758; M]

Type species: *Voluta faba* Linné, 1758; SD (M) Gray, 1847:142 (figure 73)

Diagnosis: Shell medium to large, white to colored, always patterned, biconic, distinct axial costae present; spire medium to tall; aperture narrow to moderately broad; lip thickened, distinctly denticulate; external varix present; siphonal notch present; columella with 4 strong plications occupying more than half the aperture. Type 2 animal; siphon long; mantle extension undetermined.

Description: Shell (figure 73) medium to large (adult length 6.2–38.0 mm). Color white, gray, or yellowish-olive to olive in background, always with pattern of spiral lines or rows of dots, axial lines or streaks, or variously mottled, spotted, or streaked. Shell surface smooth, glossy, with weak to usually distinct axial costae. Shape broadly to narrowly biconic, weakly to strongly shouldered. Spire medium to tall. Aperture moderately narrow to moderately broad, usually widest medially. Lip moderately to strongly thickened, distinctly denticulate, with a distinct external varix. Shell with siphonal notch weak or distinct. Posterior notch absent to weak or distinct. Shell usually without evident ventral callusing. Columella with 4 strong continuous plications occupying more than half the aperture length. Internal whorls unmodified.

External anatomy: 2 species studied. Type 2 animal; tentacles long, slender; siphon long; mantle extension undetermined; foot broad, about 1½ X shell width, 1½ X shell length; animal variously spotted, blotched, or streaked with yellow or reddish-brown. [See summary of *G. adansoni* (Kiener, 1834) in Coovert (1987g:12) and figure of *G. lucani* (Jousseaume, 1884) in Gofas & Brandao (1985:85, fig. b)].

Internal anatomy: Unknown.

Radula: Non-radulate, completely lacking buccal mass, including odontophore. 1 known non-radulate species (Coan & Roth, 1976:220).

Distribution and Habitat: Indo-Pacific (4 species), W. African (13 species). Intertidal to 183 m.

Fossil Record: Known only from the Recent.

Nomenclature, Synonymy: Various authors have designated different type species, including *M. prunum* (Gmelin, 1791) by Fischer (1883:602) and *M. bifasciata* Lamarck, 1822 by Redfield (1870:221), but the designation of *M. faba* by Gray (1847:142) was the earliest. A photograph of the type of *G. faba* has been studied (pers. obs. ex. photograph of P. W. Clover). The type of *G. nodata* was figured by Kaicher (1981:#2640). Both fall well within the limits of the genus. *Phaenospira* had previously been synonymized by Coan (1965:189).

Remarks: We consider axial costae to be a species-level character in other genera. In this case, though, *Glabella* seems to form a natural assemblage, albeit closely related to *Marginella*. Besides possessing axial costae, this group always has a strongly denticulate lip and an aperture that is broadest medially.

DISCUSSION

Family Relationships

Previous sections of this paper outlined the fundamental differences between the two families of marginelliform gastropods—the Cystiscidae and the Marginellidae. Shared similarities between each of these two families and other neogastropod families (Table 5), in particular, characters presumed to be derived, will be examined next.

The Cystiscidae have a number of unusual characters that differentiate them from the Marginellidae. Interestingly, these same characters are shared with the Olividae. The partially resorbed "cystiscid internal whorls" are characterized by being extremely thin, modified in shape, and having the columellar plications reduced to a single, axially oriented, sharp edge internally (figures 2, 3). A very similar type of internal whorl, though, is seen in members of the genus *Oliva*, clearly visible in X-ray photographs in Zeigler and Porreca (1969:8) and confirmed by personal observations of both young and adult shells of *O. sayana* Ravenel, 1834. Similar internal shell construction is found in *Agaronia* (pers. obs.). In *Olivella*, the internal whorls are often nearly completely resorbed rather than modified and thinned. For further discussion, see Olsson (1956:169), Kantor (1991:24, 41–43, 49), and Marcus and Marcus (1959:107–108). The only other gastropod families reported to have internal whorl resorption are Cypraeidae and Conidae, in which whorl walls are greatly thinned, and Neritidae and Ellobiidae, in which the internal whorls are completely resorbed (Moore, 1960:1121; Fretter & Graham, 1962: 69). Because internal whorl resorption is uncommon in gastropods, we consider this to be a shared, derived character between the Cystiscidae and Olividae.

The multiplicate columella of cystiscids consists of 1 or 2 anterior columellar plications that are reduced internally, plus parietal lirae posterior to these plications. In the Olividae, true columellar plications are absent, but a sharp, axially oriented columellar edge is found internally. The parietal area often bears distinct lirae. Although similar to the multiplicate columella of cystiscids, the olivid columella lacks anterior columellar plications.

The radular morphology is of particular interest in differentiating the Cystiscidae from the Marginellidae. The long, narrow radula of at least 80 to 200 or more rachidian plates is characteristic of the cystiscids. Lateral teeth are present only in the genus *Plesiocystiscus*, in which the radula closely resembles those of certain olivids (Olsson, 1956:figs. 9, 10). Radulae and subradular membranes of cystiscids were compared with those from: *Oliva sayana* Ravenel, 1834, *Agaronia griseoalba* (von Martens, 1897), and *Olivella (Pachyoliva) semistriata* (Gray, 1839). In all three olivid species, odontophoral cartilage hoods, very similar to those in cystiscids, were found. Separate odontophoral cartilages, each fitting into one of the flanking odontophoral cartilage hoods, were found in *O. sayana* and *A. griseoalba*. These cartilages are very similar in general shape to those of *Persicula* (figures 36, 37). These two olivids also have the posterior end of the radula, which extends beyond the odontophore, encased in a typical neogastropod radular sac and beginning as a developmental series of nascent plates. Both species have lateral teeth, but are otherwise similar in radular morphology to the cystiscid genus *Persicula* (figures 13–16). For further discussion of *Oliva* radular

Table 5. Comparison of major taxonomic characters of marginelliform groups with related neogastropod families. See text for further discussion.

Character	Volutidae	Marginel-loninae	Marginelli-nae	Cystiscidae	Olividae
Internal whorls resorbed	no	no	no	YES	YES in most
Labial lirae	absent	absent	absent	PRESENT in some	PRESENT in some
Siphonal notch	YES in some	YES in some	YES in some	YES in some	YES
Plications	continuous	continuous	continuous	multiplicate	multiplicate
Head with lateral lappets & dorsomedial channel	PRESENT in some	PRESENT	absent	absent	absent
Shell covered by mantle or foot	mantle in some	mantle (in *Afrivoluta*)	mantle	mantle in some; foot in *Canalispira*	foot
Marginellid buccal pouch	absent	PRESENT	PRESENT	absent	absent
Neogastropod radular sac	PRESENT	absent	absent	PRESENT	PRESENT
Odontophoral cartilage hoods	?	absent	absent	PRESENT	PRESENT
Radula with laterals	YES in some	no	no	YES in *Plesiocystisc.*	YES
Central rachidian tricuspid	YES in some	no	no	YES in 1 genus	YES in some
Length of radular ribbon	moderately short to long	moderately short	moderately to very short	long	long (short in *Olivella*)
Odontophoral cartilages	separate (in *Alcithoe*)	?	fused at least anteriorly	separate	separate or fused anter.
Valve of Leiblein	PRESENT	PRESENT	PRESENT or absent	PRESENT	PRESENT
Gland of Leiblein	lg. sacculate, or w/terminal bulb	lg. sacculate	with terminal bulb	short gland, no long duct	short gland, or w/terminal bulb
Duct from Gland of Leiblein	posterior to nerve ring	posterior to nerve ring	posterior or ANTERIOR	posterior to nerve ring	posterior to nerve ring
Anal gland	PRESENT	PRESENT	PRESENT	absent	PRESENT or absent
Development	direct / veliger	direct	direct	direct	most veliger

morphology, see Marcus and Marcus (1959:124–5). *Olivella* has a shorter, broader radula with laterals and separate odontophoral cartilages. Marcus and Marcus (1959: 121, fig. 31) and Kantor (1991:26, fig. 5C) further discuss the radular morphology of *Olivella*, including the odontophoral cartilages. The rachidian plates are tricuspid in *Olivella* and *Jaspidella* (Olsson, 1956:169, figs. 9, 10) and their radulae strongly resemble the triserial radulae of some *Plesiocystiscus*. *Plesiocystiscus*, the only cystiscid genus with lateral teeth, is considered to be the most primitive group in the family. Possession of lateral teeth is certainly a primitive feature, as is the tricuspid rachidian plate in cystiscids and olivids (Kilburn, 1981: 354). In summary, the entire radular morphology of certain cystiscids and olivids are very similar. Many of these features, such as the formation of the odontophoral cartilage hoods and separate, flanking odontophoral cartilages, are considered to be shared, derived characters. The common possession of a typical neogastropod radular sac is a shared, primitive character.

Additional shell features shared between cystiscids and olivids include the glossy exterior of the shell. The mantle at least partially covers the exterior of the shell in the cystiscid genera *Cystiscus*, *Granulina*, and *Pugnus*. In other cystiscid genera, such as *Plesiocystiscus*, *Gibberula*, and *Persicula*, the shell is apparently not covered by the mantle. In olivids, the foot at least partially covers the shell and affords protection, and therefore, the glossy shell exterior is apparently due to secretion by the foot, not by the mantle. A similar animal has been described for the cystiscid genus *Canalispira*. A glossy shell is apparently convergent in many groups and does not by itself suggest a strong affinity between cystiseids and olivids. A strong siphonal notch is found in the cystiscid genera *Persicula* and *Gibberula* and is very characteristic of olivids, but is also found in many other groups. Lirae on the inner surface of the outer lip are found in many species of *Persicula*, *Gibberula*, and *Canalispira*, and also in the olivid genus *Olivella*. This character is less common than the other conchological characters but still could be due to convergence. A comprehensive study and review of all these features in olivids is needed and a common link between cystiscids and olivids should be searched for in Cretaceous material.

Anatomically, both the Cystiscidae and Olividae have a valve of Leiblein and a short gland of Leiblein (with a long, convoluted duct and a terminal bulb in *Amalda*) that empties into the esophagus posterior to the nerve ring (Ponder, 1973:fig. 3). Both groups have a typical neogastropod radular sac and lack the marginellid buccal pouch. Both families have species that possess a single accessory salivary gland. These characters are also found in other neogastropods. An anal gland is absent in *Gibberula* (Ponder, 1970:71) and present or absent in the Olividae (Kantor, 1991:tables 1,2). Cystiscids have direct development, whereas olivids generally have pelagic larvae (Boss, 1982:1018).

In summary, it is suggested that the Cystiscidae and Olividae have a shared, common ancestry based on characters summarized in Table 5. They have much more in common with each other than do cystiscids and marginellids, which share no derived characters. Our recognition of two families of marginelliform gastropods reflects these conclusions. The erroneous placement of cystiseids and marginellids together was apparently based on superficially similar columellar plications, which we have shown to be completely different, and on externally glossy shells, which are a convergently derived adaptation produced by the extended mantle.

A search for the ancestry of the now restricted family Marginellidae first involves a consideration of the most primitive group within the family. Harasewych and Kantor (1991:17) suggested that the Marginelloninae may be the most primitive group in the family. This is based on the unspecialized features of the foregut, including a large valve of Leiblein lacking a glandular bypass, and the large gland of Leiblein, which lacks a terminal bulb and empties into the esophagus posterior to the nerve ring. We fully concur with this view. All other marginellids show specializations of the foregut, such as possession of a glandular bypass around the valve of Leiblein, development of a long, convoluted duct from the gland of Leiblein which has a terminal bulb, or loss of the valve of Leiblein with the duct from the gland of Leiblein passing through the nerve ring. The features of the head in *Marginellona* and *Afrivoluta*, including possession of lateral lappets and a dorsomedial channel, are features shared with many volutids (Harasewych & Kantor, 1991: 13) and are very likely derived characters. The split head in cystiscids is considered to be fundamentally different and unrelated to the dorsomedially channelled head seen in marginellonines. The two genera of the Marginelloninae were originally placed in the Volutidae based on their large shells. Another typical volutid feature in *Afrivoluta* is the placement of the anterior columellar plication which does not border the anterior edge of the columella as in all other marginellids. The presence of a weak to strong siphonal notch in the Marginelloninae is typical of volutids, but is also found in olivids and some cystiscids. All volutids and marginellids have shells with unmodified internal whorls and strong, continuous columellar plications (Moore, 1955:430; Dillon, 1981:14; Abgrall, 1981:9). A valve of Leiblein and an anal gland are present in both families (absent in some Marginellinae). All marginellids and most volutids have a relatively short radular ribbon and have lost the lateral teeth. The broad, comb-like, multiscupid rachidian plate seen in many genera of marginellids is similarly developed in *Voluta* (Weaver and DuPont, 1970:fig. 1). Apparently all marginellids have a mantle covering the external shell surface, a feature seen in some volutids. For these reasons, it is suggested that the Marginelloninae, and thus the rest of the Marginellidae, are allied to the Volutidae (Table 5). The marginellids differ in the presence of a buccal pouch.

Thiele (1929:353–356) recognized only three genera in his treatment of the Marginellidae, namely *Persicula*, *Marginella*, and *Marginellona*. These three genera, with

their included subgenera and sections, correspond very closely to the classification of the Cystiscidae and the two subfamilies of the Marginellidae presented here. The single exception is Thiele's inclusion of *Canalispira* in *Marginella*, which is not surprising due to its superficial resemblance conchologically to certain marginellids. Coan's (1965) classification recognized these three groups in name, but differed in the assignment of genera.

Ponder (1973:331) suggested that the Volutomitridae, which appeared in the Late Cretaceous, possibly arose from a common stem with the Marginellidae. Volutomitrids often have an operculum and their radula has a very odd wish-bone shaped rachidian plate, frequently with lateral teeth. These features, along with a variously sculptured shell, are very different from the marginellids. We believe that this group has little in common with the Marginellidae.

Part of the difficulty in determining familial relationships lies in the abundance of convergent characters within Neogastropoda (Ponder, 1973:302). An overall tendency toward reduction of the number of radular teeth and their cusps is seen throughout the Neogastropoda. Loss of the lateral teeth occurs in some Mitridae, Volutidae, Volutomitridae, Cancellariidae, as well as in Marginellidae and Cystiscidae. Complete loss of the radula occurs in at least some Coralliophilidae, Cancellariidae, Turridae, Terebridae, Colubrariidae, and Marginellidae. The development of a long, convoluted duct and a terminal bulb in the gland of Leiblein is seen in several families, including some Muricidae, Olividae, Volutidae, Marginellidae, and the Conoidea. The reduction or complete loss of the valve of Leiblein is less common, but is seen in some Mitridae and Marginellidae, and all Harpidae and Conoidea. Besides sharing these last two character states, the Conoidea and the Marginellidae also share the development of a buccal pouch and the passage of the duct from the gland of Leiblein through the nerve ring. All of the above characters shared by the Conoidea and Marginellidae are most likely convergent. The parallel evolution of the Conoidean "poison gland" and the gland of Leiblein in the Marginellidae was discussed by Ponder (1970:77–80), Graham (1966:146), and Fretter (1976:333–334). More research on the phylogeny of these groups is needed, as well as more study into the nature of the gland of Leiblein in the Marginellidae and its possible use as a "poison gland" (Fretter, 1976:333–334).

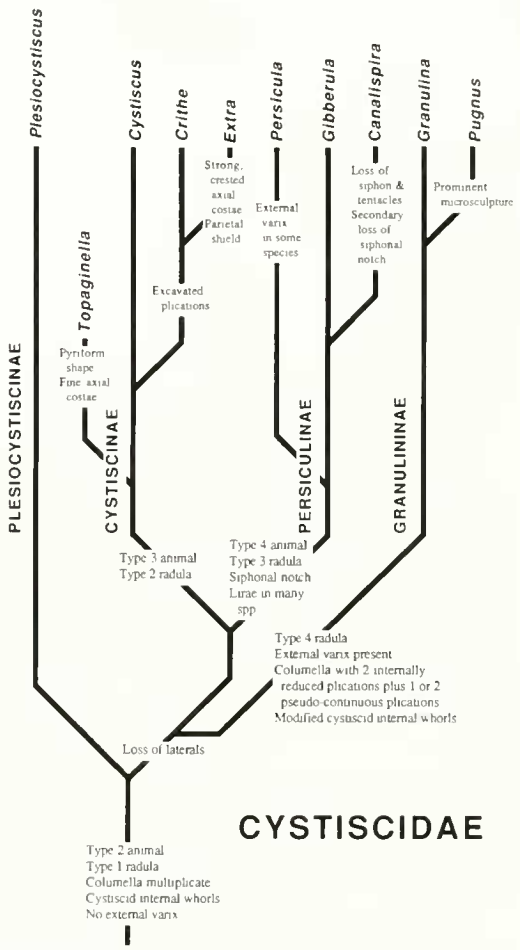


Figure 74. Intuitively derived phylogeny of the Cystiscidae. Characters at base are primitive for the family; all others are major specializations for each lineage.

Phylogeny of the Cystiscidae

Our hypothesis of the relationships of the higher taxa within the family Cystiscidae is summarized in figure 74. Presumed ancestral character states include a Type 2 animal with a cystiscid Type 1 radula, and a shell with cystiscid internal whorls, a multiplicate columella, and lacking an external varix. Additional characters include lack of a siphonal notch, presence of a valve of Leiblein, and presence of a small gland of Leiblein with a short duct emptying into the esophagus posterior to the nerve ring. All these shell and radular characters are present in the Plesiocystiscinae, here considered to be the most primitive group in this family. The presence of lateral teeth in the radula in this group, undoubtedly a primitive character state, is most significant. Some species of *Plesiocystiscus* have a tricuspid rachidian plate, another primitive feature (Kilburn, 1981:354). Because all other cystiscids have a greater number of cusps along the rachidian plate, an increase in the number of cusps is considered to be a specialization in this family. The remainder of the family have lost the lateral teeth, a derived condition also occurring in several other neogastropod families.

The unique character states that distinguish the Cystiscinae are a Type 3 animal and a Type 2 radula. *Extra* is thought to be a recent divergence from *Crithe*. The extinct genus *Topaginella*, which has a shell with fine axial costae, is likely an early offshoot from this lineage.

Persiculinae are distinguished by the presumed derived character states of a Type 4 animal, a Type 3 radula, presence of a siphonal notch, and presence of apertural lirae in many species. As *Canalispira* is thought to be a recent divergence, the absence of a siphonal notch

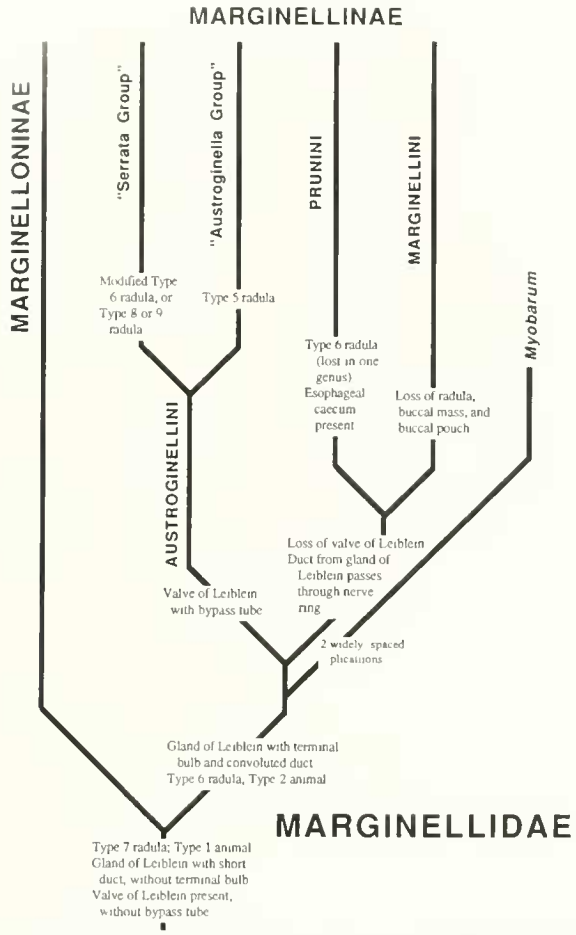


Figure 75. Intuitively derived phylogeny of the Marginellidae. Characters at base are primitive for the family; all others are major specializations for each lineage.

in this genus is hypothesized to be a secondary loss of this character. If absence of a notch is considered to be a retained primitive character, then development of a notch in the much earlier *Gibberula* and *Persicula* would have had to occur twice, which seems less likely. *Canalispira* also has a highly modified animal, lacking a siphon and tentacles. *Gibberula* is distinguished by the development of a glandular tube bypassing the valve of Leiblein, a derived character (figure 79). Development of an external varix in some species of *Persicula* is also a derived character for this family.

The Granulininae is, in some ways, the greatest departure in the family. Specializations in this group include the very distinctive Type 4 radula with modified odontophoral cartilage hoods, presence of an external varix, presence of modified cystiscid internal whorls, with the columella possessing 2 internally reduced plications in addition to 1 or 2 pseudo-continuous plications. The mantle covers the shell in this group, apparently another specialization within this family. Primitive characters that are retained include a Type 2 animal and the absence of a siphonal notch. The Granulininae is thought to have diverged from the main branch of the family (figure 74) after the lateral teeth were lost from the radula. Because this group has a fossil record dating back only to the Miocene, it could also have diverged from the plesiocystiscine line (which shares a Type 2 animal) after the cystiscines and persiculines diverged, but this would imply that lateral teeth were lost twice in this family. *Pugnus* is considered to be a recent offshoot from *Granulina*. Although the Granulininae differs in a number of characters from the other subfamilies, the Cystiscinae and the Persiculinae differ in their radically different animal types. Thus, we feel that all four groups should be accorded equal ranking as subfamilies.

Phylogeny of the Marginellidae

Our hypotheses of relationships of the higher taxa within the family Marginellidae are summarized in figures 75 and 80. Assumed ancestral characters for this family include a Type 1 animal with a marginellid Type 7 radula, a gland of Leiblein with a short duct and lacking a terminal bulb, and presence of a valve of Leiblein (figure 80). Additional characters include a shell with unmodified internal whorls, continuous columellar plications, and presence of an external varix. All these ancestral characters have been retained in the subfamily Marginelloninae, which is considered to be the most primitive group in the family. The probable relationship between the Marginelloninae and Volutidae has been discussed previously. Because a number of marginellid groups with specializations of the foregut possess fewer cusps along the rachidian plate, loss of cusps, rather than an increase in cusps (as in the Cystiscidae), is considered to be derived within this family. Further evidence of this is found in the greatly reduced radula of *Hydroginella*, a highly specialized genus, and eventual loss of the radula in two lineages of the Marginellinae. The Marginelloninae is composed of only two genera, *Afrivoluta* and *Marginellona*, which can be easily differentiated by the number and orientation of columellar plications. Lack of eyes, a development for life in deep water, and a very weak siphonal notch further distinguish *Marginellona*.

The remainder of the family is grouped together as the subfamily Marginellinae, based on the shared specializations of the gland of Leiblein, which ends in a terminal bulb and has a long, convoluted duct (figure 80). The animal is the generalized Type 2 with a Type 6 radula. The rachidian plate of the Type 6 radula has fewer cusps than the Type 7 radula. The extinct genus *Myobarum* was probably an early divergence from this main stem of the Marginellinae but could be ancestral to the entire family, based on its appearance in the late Cretaceous. The Marginellinae diverged at this point into two main lineages. The Austroginellini retained the valve of Leiblein but developed a bypass tube (figure 80). Additional characters of the Austroginellini, which are apparently primitive, include attachment of the paired salivary glands to the esophagus in front of the valve of Leiblein, and the ducts from these glands being embedded in the esophageal walls (figure 80). The other lineage,

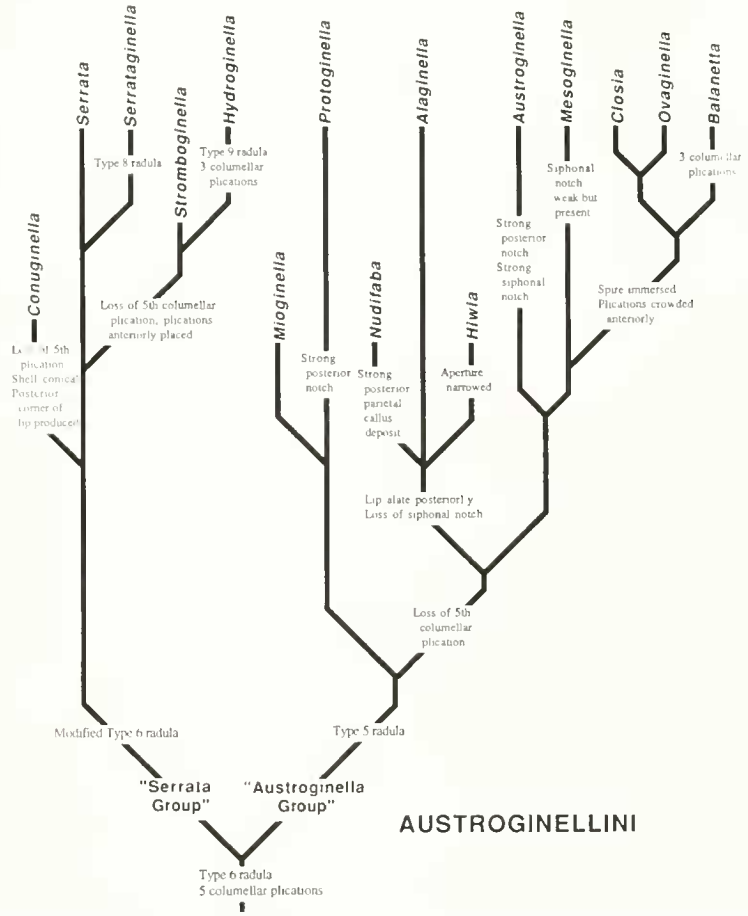


Figure 76. Intuitively derived phylogeny of the Austroginellini. Characters at base are primitive for the tribe; all others are major specializations for each lineage.

composed of the Prunini and Marginellini, lost the valve of Leiblein, but the duct from the gland of Leiblein passes through the nerve ring and empties into the extreme anterior end of the buccal cavity (figure 80). The Prunini and Marginellini are considered to be sister groups based on these shared features, with the Prunini developing an esophageal caecum, a derived character diagnostic for that tribe. Additional characters of the Prunini / Marginellini lineage, which are probably also primitive, include the paired salivary glands being free of the esophagus, and their ducts either attached to the esophagus or free, but not embedded in the walls as in the Austroginellini. The Marginellini is characterized by the complete loss of the buccal mass, including radula and odontophoral cartilages, plus the loss of the buccal pouch (figure 80). This loss also occurred in *Hyalina*, an undoubted member of the Prunini based on its possession of an esophageal caecum as well as shared conchological characters (figure 80). The loss of a radula is therefore considered to have occurred in two independent lines, not three as speculated by Coan and Roth (1976:220).

Intuitively derived phylogenetic relationships within the tribe Austroginellini are summarized in figure 76. Primitive anatomical characters for this tribe have already been mentioned. Additional conditions presumed to be ancestral include a Type 6 radula and a shell with five plications and a denticulate lip. This tribe diverged into two main lineages at this point. The "*Serrata* Group" developed a gradually weakening modified Type 6 radula, while the "*Austroginella* Group" developed a Type 5 radula, which is a narrower, fewer-cusped, chevron-shaped modification of the original Type 6 radula. (Informal groups are preferred at this level to avoid further inflation of taxonomic groupings). Within the "*Serrata* Group," the genus *Serrata* retained the modified Type 6 radula and most species retained the denticulate lip and at least a weakened fifth columellar plication. *Conuginella*, an extinct Miocene genus, lost the fifth plication and developed a distinctive conical shape and posteriorly produced lip. *Strombоginella*, another extinct genus, diverged in the Pleistocene from the lineage with anteriorly crowded columellar plications and lost the fifth plication. *Hydroginella*, also in this lineage, continued the trend of anterior crowding of plications, with the subsequent reduction to three plications. *Hydroginella* also continued the trend of radular reduction, resulting in a greatly reduced Type 9 radula. An additional specialization for this group is the presence of a collabral parietal callus

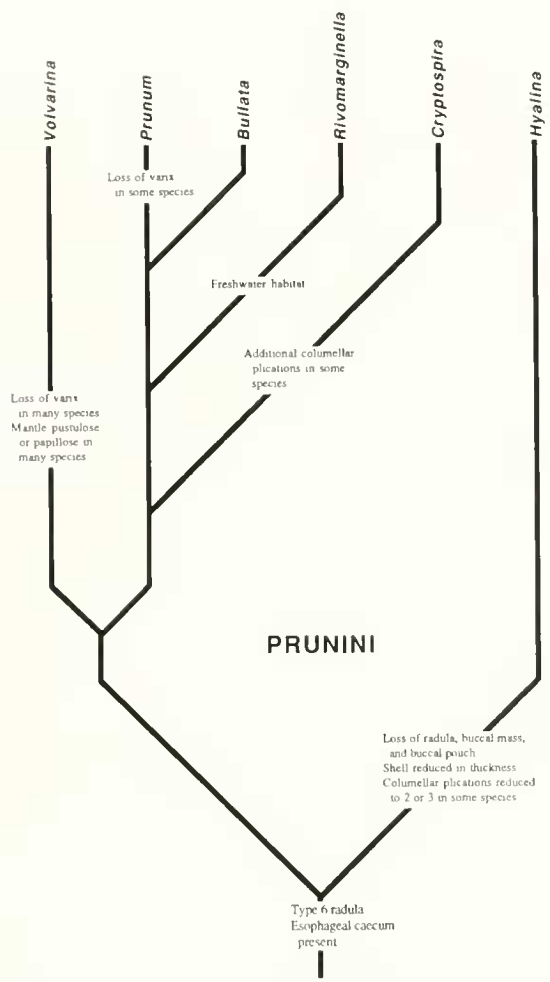


Figure 77. Intuitively derived phylogeny of the Prunini. Characters at base are primitive for the tribe; all others are major specializations for each lineage.

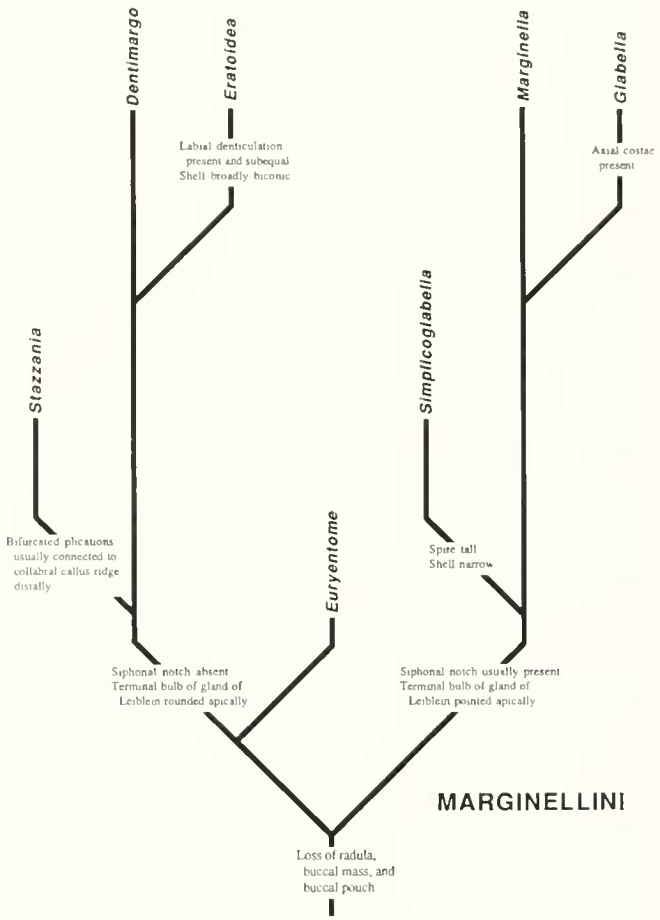


Figure 78. Intuitively derived phylogeny of the Marginellini. Characters at base are primitive for the tribe; all others are major specializations for each lineage.

ridge just posterior to the columellar plications, in which the anterior end often superficially appears to be a weak fourth plication. This derived character, along with the distinctive radula, distinguishes this well-defined genus. One species is a known fish parasite. We anticipate that additional species may also share this behavior. Shell shape, as in many groups, is variable and accounts for the many synonyms of *Hydroginella*. The genus *Serrataginella* has a very distinctive and unusual Type 8 radula. The rachidian plate possesses secondary cusps not seen in any other marginellid, giving the main cusps a serrated appearance. Unusual derived shell characters include two collabral callus ridges, one of which is confined to the aperture, and replacement of the fifth plication by a weak denticle. The "*Austroginella* Group," with a Type 5 radula, radiated into several genera. Possession of five strong columellar plications occupying more than half the aperture is ancestral within this group. *Protoginella* retained the five columellar plications and developed a strong posterior notch. An early offshoot of this branch is the extinct Eocene genus *Mioginella*, which shares the posterior notch but has carinate shoulders and a weak siphonal notch. The remainder of the "*Austroginella* Group" lost the fifth columellar plication. *Nudifaba* is an Eocene offshoot from the *Alaginella* line. *Alaginella* is characterized by a weakly to strongly alate posterior corner of the aperture, a strongly narrowed shell anteriorly, and general loss of labial denticulation in most species. This group also lacks distinct siphonal and posterior notches. Variable shape and shoulder development in this genus is responsible for the numerous genus-group synonyms. *Hiwia* is an extinct Eocene offshoot with a distinctive shell having strong axial costae and angulate or carinate shoulders. *Austroginella* is characterized by strong posterior and siphonal notches, as well as a distinctively thickened, smooth lip. *Mesoginella* is variable in shell shape and other features, has a weak or absent posterior notch, and the fourth plication is often remote. From this lineage diverged a group of genera with an immersed spire and thin, sharp, anteriorly crowded columellar plications. *Closia* and *Ovaginella* retained four plications. Strong labial denticulation was retained in *Closia*, which developed a colored shell, whereas *Ovaginella* generally lost labial denticulation

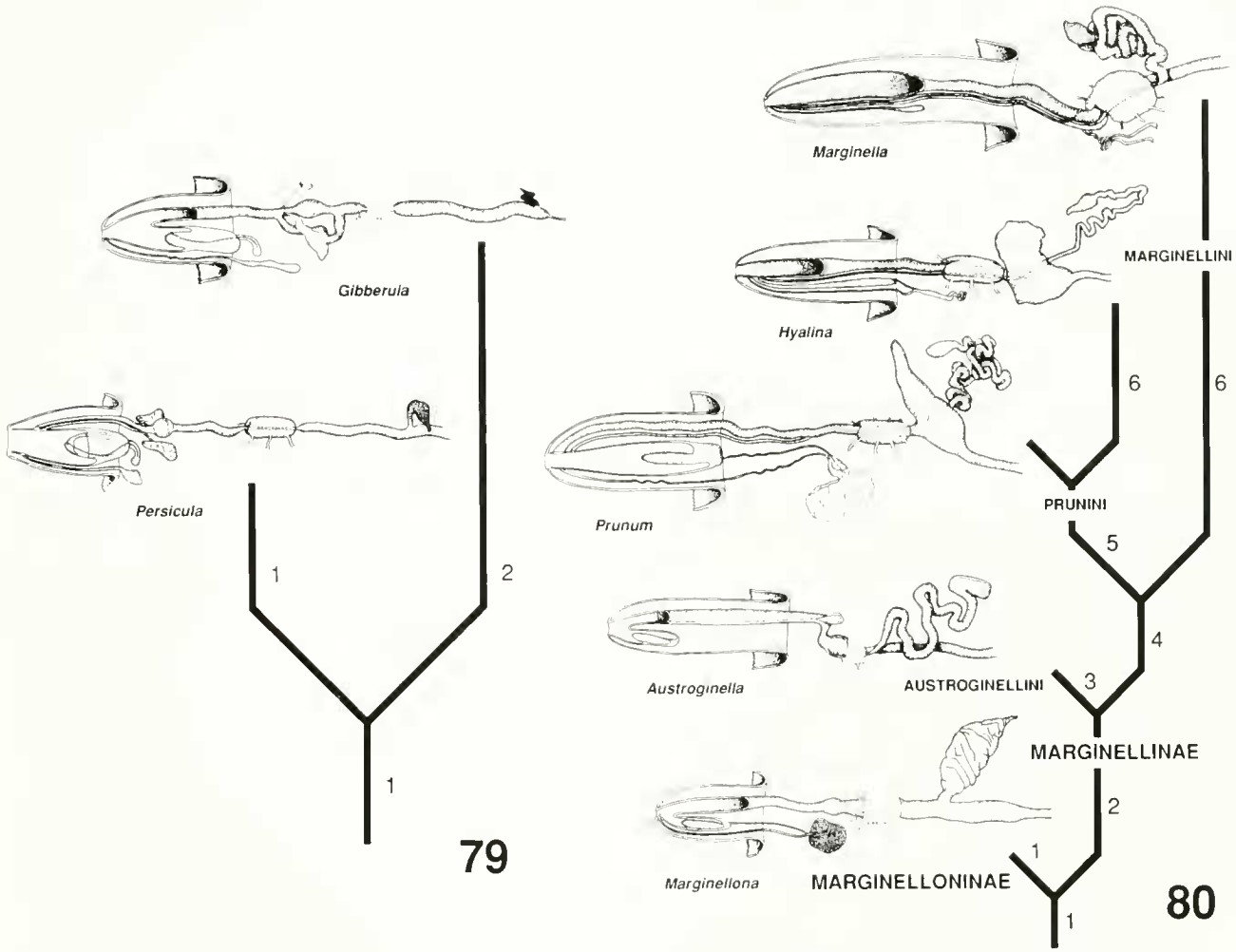


Figure 79. Intuitively derived phylogeny of the Cystiscidae, subfamily Persiculinae as illustrated by features of the foregut. Character states: 1: Valve of Leiblein without bypass tube. 2: Valve of Leiblein with bypass tube. *Gibberula* sp. after Ponder (1970), *Persicula interruptolineata* after figure 35 herein. **Figure 80.** Intuitively derived phylogeny of the Marginellidae as illustrated by features of the foregut. Character states: 1: Gland of Leiblein with short duct emptying posterior to nerve ring, valve of Leiblein present; marginellid buccal pouch present; marginellid radulae present. 2: Gland of Leiblein with terminal bulb and convoluted duct. 3: Valve of Leiblein with bypass tube; paired salivary glands attach to esophagus just anterior to valve of Leiblein; salivary ducts embedded in esophageal walls. 4. Loss of valve of Leiblein; duct from gland of Leiblein passes through nerve ring; paired salivary glands completely free of esophagus; salivary ducts attached or free, but not embedded in esophageal walls. 5: Esophageal caecum developed. 6. Loss of radula, buccal mass, and buccal pouch. *Marginellona gigas* after Harasewych and Kantor (1991), *Austroginella johnstoni* after Ponder and Taylor (1992), *Prunum aff. aletes* after figure 31 herein, *Hyalina pallida* after figure 32 herein, *Marginella glabella* after figure 34 herein.

but did not develop shell coloration. *Balanetta*, with a narrower shell, lost the fourth columellar plication.

The phylogeny of the tribe Prunini is summarized in figure 77. Anatomical features of this group have already been discussed, the most significant being the development of an esophageal caecum, a derived character state unique to this tribe. The Type 6 radula is considered primitive and is retained in nearly all genera. The widely distributed *Volvarina* lineage is characterized by loss of the external varix and development of a pustulose or papillose mantle, both occurring in many, but not all, species. The *Prunum* lineage, largely a western Atlantic radiation, has several extant Indo-Pacific species and two genera that are offshoots. *Cryptospira* developed additional columellar plications in some species, and has a variously colored or patterned shell. *Rivomarginella*, the only freshwater group, is allied to the *Prunum* lineage based on the ontogenetic development of its varix. *Bullata* is a relatively recent offshoot of *Prunum* and is confined to the western Atlantic coast of South America. Much more work is required to fully characterize *Prunum* and *Volvarina*. Attention should be focused on anatomy, including the odontophoral cartilages and radulae, external features of the animal, including coloration and mantle characters, and shell characters. Study of external varix development shows great potential and involves

cutting and polishing shell cross-sections. The final branch of the tribe Prunini is the genus *Hyalina*, characterized by the complete loss of the buccal mass, including odontophore, radula, and buccal pouch. This genus is further characterized by a thin shell and columellar plications that are reduced to two or three in some species.

Our reconstruction of the phylogeny of the tribe Marginellini is summarized in figure 78. This group is characterized by complete loss of the buccal mass and buccal pouch, and lacks the esophageal caecum of the Prunini. Shell features include four strong columellar plications spanning half or more of the aperture. One branch of this tribe is characterized by absence of a siphonal notch, and the gland of Leiblein has the terminal bulb rounded distally. Further anatomical features in *Dentimargo* include a distally pointed penis and possession of three glandular structures or seminal receptacles that join the pallial oviduct between the albumen gland and capsule gland. *Stazzania* is an extinct Eocene offshoot of the *Dentimargo* lineage characterized by the bifurcated ends of the columellar plications joining a collabral callus ridge. *Dentimargo* shells usually have a prominent posterior labial denticle that is characteristic. The shells of *Dentimargo* are also generally narrower and differ in plications, which are usually not bifurcated in Recent species. Where the plications are bifurcated, the ends do not join a collabral callus ridge as they do in *Stazzania*. *Eratoidea* is a Caribbean offshoot with subequal labial denticulation and often weak to distinct axial costae. *Euryentome* is an extinct Eocene group from the western Atlantic with a strong posterior notch and often has parietal lirae posterior to the columellar plications. The second branch of the tribe has the siphonal notch usually present, and the terminal bulb of the gland of Leiblein is pointed distally. Further anatomical differences that may differentiate this group from the *Dentimargo* line include a simple penis and only two glandular structures between the albumen gland and capsule gland. Further work is needed to confirm this in more species. *Simplicoglabella* is a Miocene offshoot with a narrower shell and a taller spire. *Marginella* is a large genus with a smooth shell, whereas *Glabella* is a well-defined group having distinct axial costae.

Extralimital Genera

The family Cryptochordidae was questionably included as an extinct subfamily of the Marginellidae by Ponder and Warén (1988:306). This family was originally named by Pchelintsev, *et. al* (1960:235) with the genus *Cryptochorda* Mörch, 1858 as type genus, and *Buccinopsis stromboides* Herrmann, 1781 as type species (OD) of the genus. Specimens of *Cryptochorda stromboides* from the Eocene of France were examined and this species is unrelated to either the Cystiscidae or the Marginellidae. This species has a tiny protoconch, a strong siphonal notch, irregularly-spaced axial costae, a weak siphonal fasciole, and the columella is bordered by a sharp edge with no columellar plications otherwise evident. The glossy shells have some parietal callusing and a sharp posterior sinus. These are all characters of the Harpidae, and we would therefore agree with the assignment of *Cryptochorda* to that family by Palmer and Brann (1966: 616–617). This group can be removed from further consideration in the Cystiscidae or Marginellidae.

Bouchet (1989:82–83) placed the monotypic genus *Tateshia* Kosuge, 1986 (type species *T. yadai* Kosuge, 1986, OD) in the Marginellidae and regarded it as a marginellid with a primitive radula. We initially regarded this genus as a marginellid based on shell morphology but assumed an error had occurred in associating the radula, which is very muricid-like, a fact noted by Kosuge (1986: 78). We have been informed by Dr. Sadao Kosuge (pers. comm.) that radulae were obtained from three specimens and thus it appears no error occurred. This genus was originally placed in the Olividae by Kosuge. We can only conclude that this species, which has a radula unlike any member of the Cystiscidae or Marginellidae, belongs elsewhere. Perhaps further anatomical work will clarify the relationship of this enigmatic genus, which, admittedly, has a very marginellid-like shell.

Argentovoluta Vazquez and Caldini, 1989 (type species *A. bottai* Vazquez & Caldini, 1989) was mentioned by Poppe and Gotto (1992:215) as possibly belonging to the Marginellidae. The columellar plications are clearly volutid and, therefore, this genus can be removed from further consideration in the Cystiscidae or Marginellidae.

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